

Research Report

# Hemispheric metacontrol and cerebral dominance in healthy individuals investigated by means of chimeric faces

Cosimo Urgesi<sup>a</sup>, Emanuela Bricolo<sup>b</sup>, Salvatore M. Aglioti<sup>c,\*</sup>

<sup>a</sup>*Dipartimento di Scienze Neurologiche e della Visione, Sezione di Fisiologia Umana, Università degli Studi di Verona, Verona, Italy*

<sup>b</sup>*Dipartimento di Psicologia, Università degli Studi di Milano-Bicocca, Milano, Italy*

<sup>c</sup>*Dipartimento di Psicologia, Università di Roma “La Sapienza” and IRCCS Fondazione Santa Lucia, Via dei Marsi 78, 00185 Roma, Italy*

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## Abstract

Cerebral dominance and hemispheric metacontrol were investigated by testing the ability of healthy participants to match chimeric, entire, or half faces presented tachistoscopically. The two hemi-faces compounding chimeric or entire stimuli were presented simultaneously or asynchronously at different exposure times. Participants did not consciously detect chimeric faces for simultaneous presentations lasting up to 40 ms. Interestingly, a 20 ms separation between each half-chimera was sufficient to induce detection of conflicts at a conscious level. Although the presence of chimeric faces was not consciously perceived, performance on chimeric faces was poorer than on entire- and half-faces stimuli, thus indicating an implicit processing of perceptual conflicts. Moreover, the precedence of hemispheric stimulation over-ruled the right hemisphere dominance for face processing, insofar as the hemisphere stimulated last appeared to influence the response. This dynamic reversal of cerebral dominance, however, was not caused by a shift in hemispheric specialization, since the level of performance always reflected the right hemisphere specialization for face recognition. Thus, the dissociation between hemispheric dominance and specialization found in the present study hints at the existence of hemispheric metacontrol in healthy individuals.

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## 1. Introduction

Studies on the functional specialization of the cerebral hemispheres indicate that the left hemisphere (LH) and the right hemisphere (RH) map linguistic and spatial functions respectively [8]. Behavioral studies in which visual stimuli are channeled to the LH or to the RH of healthy individuals indicate, for example, that the latter is specialized in processing faces [22,35]. In a similar vein, brain lesion [1] and neuroimaging studies [10,17,18] suggest that specific neural structures, in particular the right fusiform gyrus,

subserve face perception. It is important to clarify here that the term hemispheric specialization (or hemispheric ability) indicates the functional advantage of each hemisphere in processing a given type of stimulus (e.g., linguistic vs. spatial), and the term hemispheric dominance the tendency of each hemisphere to assume control of a given sensorimotor or cognitive task. Interaction and communication between the two cerebral hemispheres are necessary for integrating sensory, motor, and cognitive functions into unitary and efficient behavioral responses [15]. Lateralized tachistoscopic studies, which compare the level of performance (quantitative differences) or the strategies (qualitative differences) used by the two cerebral hemispheres in the processing linguistic or spatial stimuli projected in one visual hemi-field, allow us to determine the relative hemi-

\* Corresponding author.

*E-mail address:* [salvatoremaria.aglioti@uniroma1.it](mailto:salvatoremaria.aglioti@uniroma1.it).

*URL:* <http://w3.uniroma1.it/aglioti/> (S.M. Aglioti).

spheric specialization. On the other hand, experimental conditions in which stimuli are channeled to both cerebral hemispheres (bilateral presentations) allow to investigate the extent to which each hemisphere influences the performance in a given task [11].

The first demonstration of possible dissociations between hemispheric specialization and hemispheric dominance was observed in split-brain patients, in whom the corpus callosum had been surgically sectioned for control of drug-resistant epilepsy [24]. Levy et al. [24] presented chimeric faces tachistoscopically for 150 ms; the faces were obtained by juxtaposing complementary half faces of different individuals. The two half figures were joined at the vertical meridian of the visual field; thus, each half was sent to the contralateral hemisphere. Split-brain patients did not notice that stimuli were chimeric and reported that complete figures were presented. Remarkably, however, when asked to point to one out of several different drawings of faces, independently of the hand used for pointing patients chose the face corresponding to the left-half stimulus (LHS), which projects to the RH. In contrast, when asked to verbally report the experimental stimulus, patients described or named the face corresponding to the right-half stimulus (RHS), which projects to the LH. Thus, changes in the response modality determined changes in hemispheric dominance. However, performance in the naming condition was rather poor possibly because the dominant LH is not specialized for processing faces. These results suggest that the most skilled hemisphere does not always assume control of performance in a given cognitive task. Indeed, dynamic factors (e.g., the modality of response) may induce the non specialized hemisphere to dominate performance, even if the lack of specialization has detrimental effects on performance. That hemispheric specialization and dominance may be dissociated suggests that cerebral dominance is not determined only by the extent to which each hemisphere has superior ability in performing the task. According to Levy and Trevarthen [23], the dissociation between hemispheric dominance and specialization points to the existence of a choice-mechanism, called hemispheric metacontrol, that determines which hemisphere holds sway in a given cognitive operation.

These classic, pioneering studies indicate that, although the behavior of split-brain patients under daily life conditions appears unitary, the two separated hemispheres may process sensory information independently from one another [8]. Moreover, these studies suggest that the corpus callosum may have to do with brain mechanisms that suppress several types of conflicting information, perhaps with the aim of creating a unitary representation of the perceptual world. Interestingly, a mechanism similar to the hemispheric metacontrol described in split-brain humans was recently demonstrated in split-brain monkeys [19].

That metacontrol is not merely an abnormality of the split-brain condition is suggested by a series of studies in healthy individuals in whom accuracy in processing spatial

or linguistic stimuli was examined when information about the same stimulus reaches simultaneously the two hemispheres [12,13]. For example, Hellige et al. [13] asked healthy individuals to identify nonsense syllables presented to the left or to the right hemi-field (unilateral condition), or simultaneously to both visual fields (bilateral condition). The qualitative error pattern in the two unilateral conditions was different, thus showing that the two hemispheres handle this task by using different strategies of processing. Moreover, performance was better in the right hemi-field than in the left hemi-field condition, because the strategy employed by the LH in processing linguistic stimuli is more efficient. Surprisingly, the error pattern in bilateral trials was similar to the error pattern during left hemi-field presentations and different from the error pattern during right hemi-field presentations. That the mode of processing of the RH was used in bilateral condition would indicate that, when both hemispheres have simultaneous access to the same stimulus information, the dominant hemisphere is not necessarily the one specialized for the type of stimulus presented [13]. Thus, the existence of hemispheric metacontrol in healthy individuals was suggested in conditions that induced a conflict between the strategies of processing employed by the two hemispheres. No studies, however, have so far demonstrated dissociations between hemispheric specialization and dominance under conditions of striking perceptual conflicts of the stimuli sent to the two cerebral hemispheres.

Few studies using chimeric stimuli have addressed the issue of whether and under which circumstances suppression of perceptual conflicts takes place in healthy individuals. Milner and Dunne [29], for example, found that healthy individuals judged chimeric stimuli presented for only 100 ms as entire when the junction line between half figures was not visible, a condition in which completion of the LHS or of the RHS took place irrespectively of the response modality. In a similar vein, Yovel et al. [44] used chimeric faces in which the line of junction of the two halves was covered with a white stripe. Moreover, they used stimuli in which the contrast of one half stimulus was reduced. When these stimuli were presented in central vision for 60 ms, participants perceived all face stimuli as bilaterally complete. These data suggest that the spatial arrangement of each half face facilitates the suppression of incongruence between visual images projected simultaneously to the two hemispheres.

The suppression of incongruence between the two halves used to compound chimeric faces was less efficient when split-brain patients were suddenly asked to change the type of response, for example from naming to pointing and vice versa [24]. This anecdotal result suggests that in delayed response conditions suppression of the discrepancy between the two sides of chimeric stimuli is more difficult. However, little is known about the influence of temporal variables on suppression of perceptual conflicts and hemispheric metacontrol. By means of event-related potentials, Terasaki and

Okazaki [38] estimated that the conduction time of visual information transfer via the corpus callosum equals 18 ms. As interhemispheric integration is a process which requires time, it is possible that merging incongruent features into a unitary percept occurs only when the two halves of chimeric stimuli are presented simultaneously to both hemispheres. The RH advantage for facial processing may be related to the single cell recording study in humans in which it is demonstrated that during a face matching task neurons in the right anterior temporal lobe fire earlier than neurons in the left right anterior temporal lobe [27]. Since the timing of neural responses may be one factor accounting for the RH dominance in face processing, the asynchronous stimulation of the two cerebral hemispheres may influence the hemisphere that controls the face matching task. Thus, the precedence of hemispheric stimulation may induce a dynamic shift of cerebral dominance.

The present study was aimed at investigating the role of timing of hemispheric stimulation on interhemispheric interaction. To deal with this issue, two experiments in which the two half figures forming chimeric faces were presented simultaneously (Experiment 1) or asynchronously (Experiment 2) were carried out. Thus, we tested the effect of variables such as exposure time (ET) and spatial arrangement of half faces on interhemispheric integration. Notably, the very short ETs used in the present series of experiments allowed assessing the temporal windows in which suppression of conflicts in the chimeric stimuli occurred in healthy individuals. Moreover, an entirely novel set of phenomena concerning the influence of the asynchronous stimulation of the two hemispheres on interhemispheric integration and hemispheric metacontrol was explored here by presenting half stimuli compounding chimeric or entire faces separated by different time intervals.

All participants were native Italian speakers with normal or corrected to normal visual acuity in both eyes and with no history of neurological or psychiatric illnesses. Participants were naive as to the purposes of the experiment and information about the experimental hypothesis was provided only after the behavioral tests were completed. All participants gave their informed consent to participate in the study and the procedures were approved by the local ethics committee.

## 2. Experiment 1

Experiment 1 aimed to verify whether or not healthy individuals suppress the discrepancy in chimeric faces presented for very brief ETs. Moreover, we were interested in analyzing the possible implicit processing of the suppressed half (i.e., the half face that is not reported in the response). To this end, the two halves forming the chimeric faces were presented simultaneously at various ETs.

### 2.1. Materials and methods

#### 2.1.1. Participants

Sixteen healthy volunteers (12 women and 4 men), ranging in age from 19 to 29 years ( $M = 22.8$  years), participated in this experiment. A standard handedness inventory [4] allowed ascertaining that 11 participants were right-handed, 2 were left-handed, and 3 were ambidextrous.

#### 2.1.2. Stimuli and apparatus

The experimental stimuli were created using four color photographs, each displaying a face with a neutral expression. The models in the photographs were four young males (mean age = 24.5 years) unfamiliar to the participants. The digital photos were modified by means of Adobe Photoshop 4 and were matched with respect to luminance and crude contours. Photos were cut along the midline and the resulting halves of each model were joined with the complementary half faces of the other models. Thus, 12 chimeric stimuli were obtained. Stimuli subtended  $3.64^\circ \times 3.94^\circ$  of visual angle and were presented on a white background with an outermost edge  $1.82^\circ$  from fixation. A random-dot mask was obtained by scrambling the corresponding face stimulus by means of a custom-made image-segmentation software.

Participants sat 57 cm away from a 17-in. monitor (resolution:  $1024 \times 768$  pixels, refresh frequency: 99 Hz) of a G4 Apple computer. Stimulus-presentation timing and randomization were controlled by a custom software written by using Matlab (The MathWorks, Inc., MA, USA) and the Psychophysics Toolbox extensions [2]. During the experiment, all participants had their chin and forehead restrained and their head aligned with the center of the viewing screen. Eye position was monitored and fixation was checked continuously during tachistoscopic presentation by means of a rearview mirror. Trials in which head or eye movements were detected during the presentation of the target (2.3% of the total) were repeated in the same block in random order.

#### 2.1.3. Procedure

Participants were tested in a single experimental session lasting approximately 30 min. On each trial, participants were asked to match a facial target stimulus presented tachistoscopically with one out of four different probe stimuli. The experimental session consisted of 18 blocks, each containing 20 trials (the 12 chimeric faces and the 4 entire faces repeated twice). The order of trials within a block was randomized for each participant. The different ETs used were as follows: 10, 20, 30, 40, 50, 60, 70, 80, and 90 ms. Two separate blocks of trials were presented for each ET. Based on preliminary results suggesting that most participants suppress the discrepancies between the two halves of chimeric faces at ET up to 40 ms, a Latin-square balancing of the 10-, 20-, 30-, and 40-ms-ET blocks was used to control for order and practice effects. At the end of these first eight blocks, 10 additional blocks of trials were

presented at 50, 60, 70, 80, and 90 ms ET, according to an increasing ET order with the aim of determining the exact exposure duration which induced detection of conflicts in each participant.

A trial started with the presentation of a fixation point (lasting 500 ms) followed by the target stimulus. Image persistence was limited by means of the 500-ms mask; soon after the disappearance of the mask, the four entire faces were presented along the vertical meridian (Fig. 1). The position of the four probe stimuli was randomized and they remained on the screen until a response was made. Participants were asked to respond as quickly as possible by using their index finger to press one out of four keys (marked on a standard computer keyboard). Each key corresponded to one of the four locations on the screen where the probe stimuli were presented. After the presence of chimeric faces was overtly detected, participants pressed a key each time he/she thought a stimulus was chimeric (in addition to the four keys used for matching the non chimeric stimuli). Eight participants used their right hand, and the remaining 8 used their left hand. RTs and accuracy were recorded and stored for automatic analysis.

During the experiment, no mention was made at any time of the possibility that the stimulus presented tachistoscopically was chimeric. To assess the instant at which the chimeric nature of the stimuli was discovered, at the end of each block, each participant was encouraged to report on the experimental stimuli. Moreover, each subject was specifically asked whether: (1) he/she noticed anything peculiar in the experiment and the stimuli; (2) he/she noticed any difference

between the target stimulus and the matching probe stimulus; (3) he/she noticed any target stimulus that was not comprised in the set of probes. When participants reported affirmative responses to any of these questions, they were considered as being aware of the chimeric nature of the stimuli. According to a subjective criterion for conscious perception [14,28], the absence of reports that something peculiar was in the experiment and the stimuli, and negative responses to all the questions indicated that processing of conflicting information occurred at an unconscious level.

#### 2.1.4. Data analysis

Data were analyzed by means of different analyses of variance (ANOVAs). Post hoc multiple comparisons were carried out by means of the Newman–Keuls test. On chimeric trials, responses were considered correct if they corresponded to either the RHS or to the LHS. Thus, the chance level was 50% for chimeric and 25% for entire faces. To compare participants' accuracy in responding to chimeric and entire faces, a standardized index of accuracy was computed using the following formulas:  $AI_C = [(P_C - 0.5) / (1 - 0.5)] \times 100$ ; and  $AI_E = [(P_E - 0.25) / (1 - 0.25)] \times 100$ , where  $AI_C$  and  $AI_E$  are the accuracy indexes,  $P_C$  and  $P_E$  are the proportions of correct trials, and 0.5 and 0.25 is the chance level for chimeric and entire faces respectively. Thus, both for chimeric and entire faces, a value of 0% indicates that performance is at chance level.

Mean RTs in matching chimeric and entire faces were calculated at each ET. Only RTs for correct trials were considered; moreover, trials with RTs lower than 1000 ms

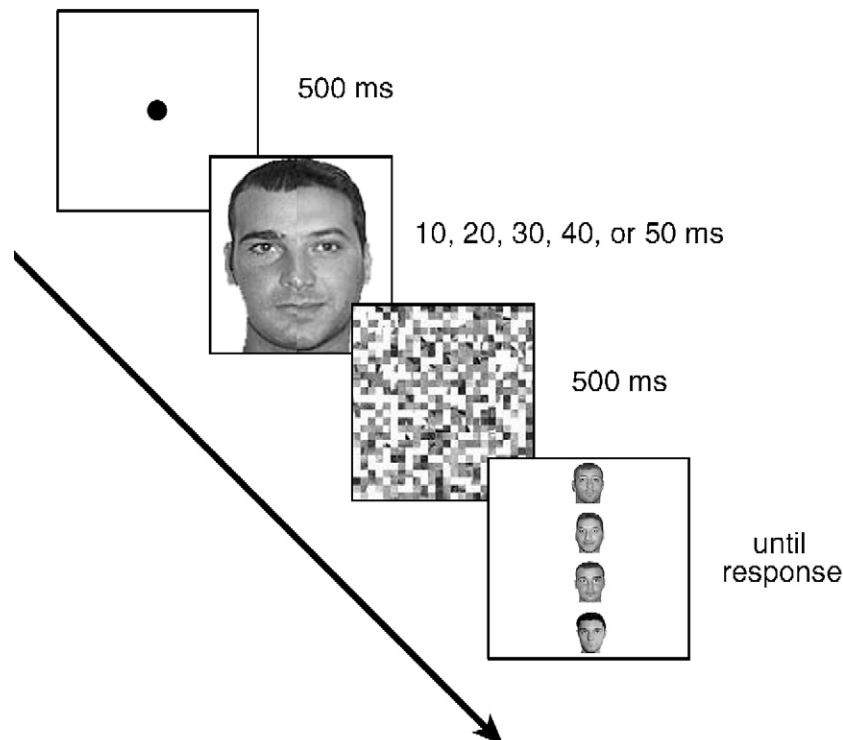


Fig. 1. Trial events in Experiment 1. As shown in the figure, the target face could be presented for 10, 20, 30, 40, or 50 ms in different blocks of trials.

(6.2%) and higher than 5000 ms (7.1%) were considered as anticipations and retards respectively and were not included in the RT, accuracy, and laterality indexes analysis.

For each block, the percentage of correctly matched chimeric trials where participants chose the probe stimulus corresponding to the LHS was considered as an index of the response asymmetry (laterality index). A laterality-index value of 50% indicates that LHS matches equal RHS matches. Values significantly higher than 50% indicate a preference towards the LHS (RH dominance); values significantly lower than 50% indicate a preference towards the RHS (LH dominance). Analyses of the laterality index were performed by means of a series of one-sample *t* tests (two-tailed). An alpha level of .05 was used for all statistical tests.

## 2.2. Results

No participant detected the presence of chimeric faces at ETs of 10, 20, 30, or 40 ms; the presence of chimeric faces was detected at the 50 ms ET by 2 participants, at the 60 ms ET by 7 participants, and at the 90 ms ET by the remaining 7 participants. It was observed that on most chimeric trials participants showed behavioral responses such as wry facial expressions or frowning. In blocks with ETs higher than 40 ms, participants often reported that most stimuli were *strange*. All these reports typically preceded complete awareness of the real nature of the chimeric faces.

Once the presence of chimeric faces was overtly detected, participants were able to identify this type of stimulus in 75.4% of the trials. Entire faces were labeled as chimeric in only 3.7% of entire-face trials, thus ruling out a response bias towards chimeric stimuli. It is worth noting, however, that the tendency to say “chimeric” in conditions of uncertainty may simply reflect the higher frequency of chimeric trials. Accuracy indexes, RTs, and laterality indexes in the blocks (namely, ETs of 10, 20, 30, and 40 ms) where the presence of chimeric stimuli went undetected were entered in different ANOVAs.

### 2.2.1. Accuracy index

An ANOVA with responding hand (left, right) as between-subjects variable and type of stimulus (chimeric, entire faces) and ET (10, 20, 30, 40 ms) as within-subjects variables was performed on the accuracy indexes. Type of stimulus was significant [ $F(1,14) = 23.56, P < 0.001$ ], since accuracy was higher for entire faces (62.06%) than for chimeric faces (45.77%). The significance of ET [ $F(3,42) = 31.48, P < 0.001$ ] was due to the increase of accuracy at longer ETs. Post hoc tests showed the following: accuracy improved significantly between 10 ms (25.84%) and 20 ms ET (50.58%,  $P < 0.001$ ) and between 20 ms and 30 ms ET (64.87%,  $P = 0.01$ ), while the improvement was only marginally significant between 30 ms and 40 ms ET (74.35%,  $P = 0.08$ ). Responding hand [ $F(1,14) = 2.15, P = 0.165$ ] and interactions were not significant. The insignificance of the interaction type of

stimulus  $\times$  ET [ $F(3,42) = 1.07, P = 0.379$ ] is explained by the fact that the increase of accuracy as ETs increased was comparable for chimeric and entire faces (Fig. 2). This effect was confirmed by a trend analysis showing that the curve which best fitted the actual distribution was linear for both chimeric [ $F(1,14) = 56.34, P < 0.001$ ] and entire faces [ $F(1,14) = 71.04, P < 0.001$ ].

### 2.2.2. RTs

An ANOVA with responding hand as between-subjects variable and with type of stimulus and ET as within-subjects variables was performed. The main effect of type of stimulus was significant [ $F(1,14) = 15.85, P = 0.001$ ], since responses to entire faces (2067.31 ms) were faster than those to chimeric faces (2303.06 ms). The main effects of responding hand and ET were not significant ( $F < 1$ ). Interestingly, the interaction type of stimulus  $\times$  ET [ $F(3,42) = 4.91, P = 0.005$ ] was significant since RTs to entire faces were faster than those to chimeric faces at all but 10 ms ET. Participants were faster in matching entire faces as ET increased, while no change according to increases in ETs occurred for chimeric faces (Fig. 3). No other interaction was significant.

### 2.2.3. Laterality index

Series of one-sample *t* tests were used to assess whether or not the laterality indexes at each ET were significantly different from 50% (a value where LHS matches equal RHS matches). As shown in Table 1, the laterality indexes differed significantly from 50% at all ETs; participants showed a preference for choosing probe stimuli corresponding to the LHS. An overall RH dominance for faces was observed in 13 of 16 participants, with no apparent relation to handedness and gender. An ANOVA with responding hand as between-subjects variable and ET as within-subjects variable was performed on laterality indexes. The main effect of responding hand [ $F(1,14) = 2.26, P = 0.155$ ], ET [ $F(3,42) = 1.07, P = 0.371$ ] and their interaction [ $F(3,42) = 0.44, P = 0.724$ ]

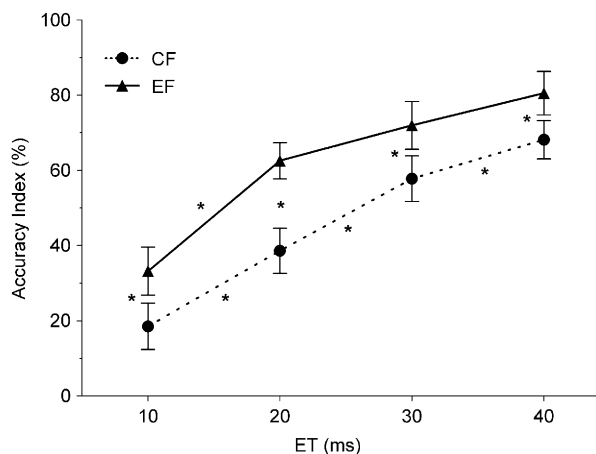


Fig. 2. Accuracy indexes in matching chimeric faces (CF, stippled line) and entire faces (EF, continuous line) in Experiment 1. Means ( $\pm$ SE) are plotted according to exposure time (ET). \* $P < 0.05$ .

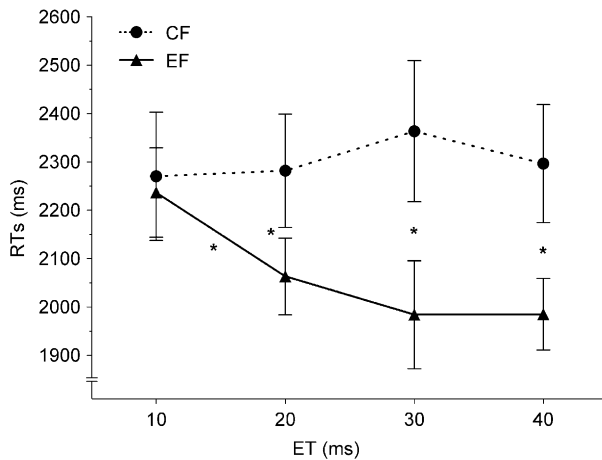


Fig. 3. Reaction times (RTs) in matching chimeric faces (CF, stippled line) and entire faces (EF, continuous line) in Experiment 1. Means ( $\pm$ SE) are plotted according to ET. \* $P < 0.05$ .

were not significant. The insignificance of the main effect of responding hand indicates that the RH was dominant in the face matching task independently of which hand was used to respond.

### 2.3. Discussion

The main result of the present experiment is that the presentation of stimuli for very brief ETs prevented healthy individuals from detecting the conflicting information carried by the chimeric faces. No participant overtly detected the presence of chimeric faces for ETs up to 40 ms. Since the ET order was balanced across participants, the greater ability to detect chimeric faces contingent upon an increase in ET was likely due to genuine processing of the stimuli instead of practice effects with the experimental stimuli and tasks. The large variability in the exact ET necessary for explicitly reporting the presence of chimeric faces is likely to reflect a number of inter-individual differences involving not only the ability to process facial stimuli but also the criteria adopted to perform the task.

Like split-brain patients [24], healthy participants suppressed the perceptual conflict in the stimulus by completing one half face at a completely unconscious level. Notably, however, although the discrepancy was not consciously perceived, it affected performance. Indeed, performance was lower in matching chimeric than entire faces. Lower accuracy and longer RTs in chimeric trials may reflect the additional processing required to suppress the emergence of conflicts at an explicit level. The increase in accuracy contingent upon ETs was parallel for chimeric and for entire faces, thus suggesting that comparable mechanisms and strategies were involved in matching the two types of stimuli. Notably, in most of the chimeric trials, although participants were unable to overtly report the conflict between the half figures, they screwed up their faces, smiled wryly, or frowned. Before the conflicts were

detected, when participants were specifically asked about the reasons for their facial expressions, they typically attributed their behavior to the task difficulty. Importantly, formal interviews carried out at the end of the experiment revealed that no participant had realized that the stimuli could be chimeric before explicit detection of their presence was made. The facial behaviors on chimeric trials in blocks with 40 ms ET or lower converge with the impairment of performance on chimeric trials to indicate that conflicting information was processed at an unconscious level.

Participants showed a strong preference in choosing the probe stimulus corresponding to the LHS, which projects to RH. This clear evidence for RH dominance is in keeping with studies employing chimeric faces [9,25,29,36] and the lateralized presentation of facial stimuli [22,35]. Thus, results indicate that presentation of chimeric stimuli for brief ETs allows studying cerebral dominance when there is no awareness of interhemispheric discrepancies.

### 3. Experiment 2

Anecdotal evidence suggests that suppression of incongruence between the two sides of chimeric stimuli was more difficult when split-brain patients, previously instructed to make a pointing response, were abruptly requested to make a verbal response or vice versa [24]. Thus, the presence of chimeric stimuli was noticed more easily under conditions of delayed response where more time was allowed for interhemispheric communication. The main aim of Experiment 2 was to study whether the detection of conflicts and interhemispheric interaction and hemispheric metacontrol were influenced by an unusual presentation of chimeric or entire facial stimuli. An entirely novel experimental paradigm in which the two halves of entire or chimeric faces were presented at different stimulus-onset asynchronies (SOAs) was used. Although this modality of presenting facial stimuli has never been used before, it allows testing whether comparable detection of the intrinsic discrepancy of chimeric faces occurs at comparable ETs for simultaneous and sequential presentation of half stimuli. This procedure may also influence the hemisphere that holds sway in the response, thus possibly inducing a dynamic shift of cerebral dominance according to the precedence of hemispheric

Table 1  
Laterality indexes at each exposure time (ET) in Experiment 1

| ET (ms) | <i>M</i> (%) | SE  | <i>t</i> | df | <i>P</i> |
|---------|--------------|-----|----------|----|----------|
| 10      | 58.5         | 3.2 | 2.65     | 15 | 0.018    |
| 20      | 58.9         | 3.5 | 2.52     | 15 | 0.023    |
| 30      | 60.6         | 3.5 | 3.05     | 15 | 0.008    |
| 40      | 64.9         | 3.8 | 3.96     | 15 | 0.001    |

Note. Mean values of 50% indicate that left choices were identical to right choices. Values higher than 50% indicate that more left-half stimuli were matched; this effect can be attributed to the RH specialization in processing unfamiliar faces. Series of one-sample *t* tests (two-tailed) were used.

stimulation. While the amount of LHS matches (laterality index) indicates hemispheric dominance, the quantitative level of performance, both in terms of RTs and accuracy, allows us to ascertain whether or not possible changes of hemispheric dominance are accompanied by corresponding reversals of hemispheric specialization. We hypothesize that a possible reversal of cerebral dominance should not be followed or accounted for by a corresponding reversal of hemispheric specialization. The possible dissociation between hemispheric specialization and dominance would demonstrate the existence of hemispheric metacontrol in healthy individuals under conditions of interhemispheric perceptual conflicts.

### 3.1. Materials and methods

#### 3.1.1. Participants

Participants were 22 healthy volunteers (18 women and 4 men), with a mean age of 23.6 years (range: 19–30 years). A standard handedness inventory [4] indicated that all participants were right-handed. Participants were randomly assigned to one of two groups according to the hand, left or right, used to perform the experimental task. No individuals had participated in Experiment 1.

#### 3.1.2. Stimuli, apparatus, and procedure

The experimental session lasted about 60 min and consisted of six blocks of trials. Fifty-six stimuli were randomly presented in each block: 24 chimeric faces, 16 entire faces, 8 left-, and 8 right-half faces. Models' half faces used in the previous experiment could be presented with the complementary half of the mask stimulus (half faces), with the complementary half face of the same model (entire faces) or of the other models (chimeric faces). Although no mention of the presence of chimeric faces was made, participants were informed that half faces could be presented and were instructed to pay attention to both left and right sides of the fixation point. By including half-face trials, we prevented participants from focusing only on the half stimulus preceding or following the other one.

Response modality and experimental procedure were as in Experiment 1. Unlike Experiment 1, and previous studies using chimeric stimuli [29,36], in Experiment 2, each half face forming the target stimuli preceded or followed the other half (Fig. 4). As shown in Experiment 1, performance was high for both chimeric and entire faces, and no participant consciously detected the presence of chimeric faces at a 30 ms ET. Thus, each half face was presented for 30 ms. Six SOAs between each half stimulus, namely, 10,

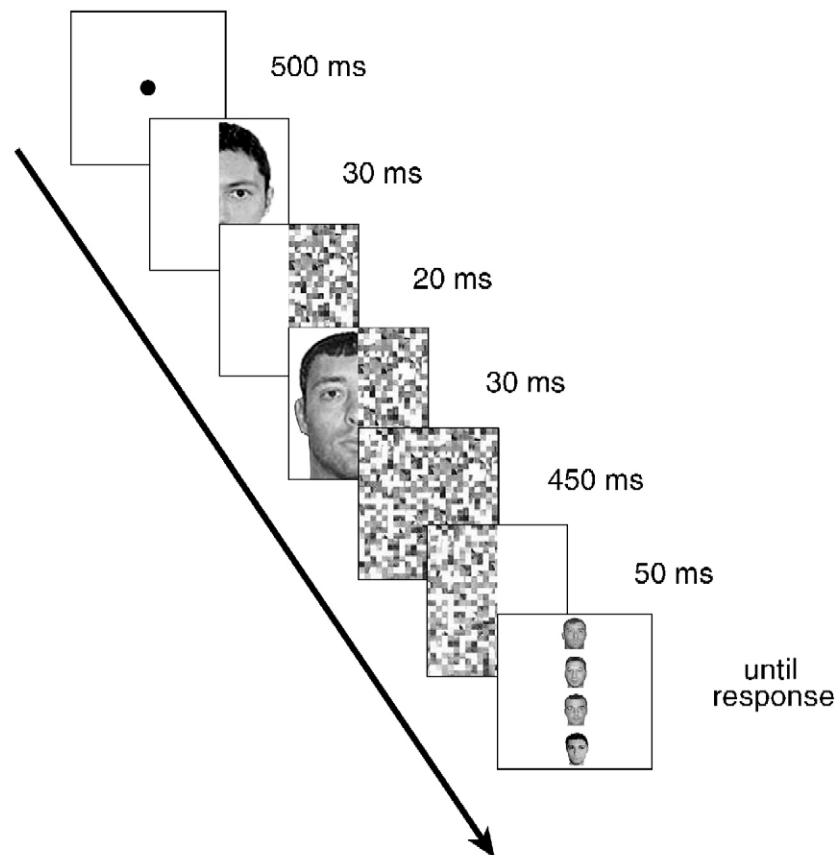


Fig. 4. Schematic representation of the trial events in Experiment 2 for a chimeric trial in the right-first condition with an asynchrony interval of 50 ms. In the case of half-faces trials, half-mask stimulus instead of a half face was presented. Note that the duration of each hemi-figure was independent from the presence of the complementary one.

20, 30, 40, 50, and 100 ms, were used in separate blocks of trials. At 10 and 20 ms SOA, the second half appeared when the first one was still on the screen; at 30 ms SOA, the second half appeared simultaneously when the first half disappeared; at 40, 50, and 100 ms SOA, the second half appeared 10, 20, or 70 ms after the first half disappeared. The time from the appearance of the first half stimulus to the disappearance of the second half never exceeded 130 ms (at 100 ms SOA) and thus was always less than the average latency of saccadic eye movements. The first block was at 10 ms SOA, and an increasing SOA order was followed in all participants. On half of both chimeric- and entire-face trials, the left side of the target stimulus preceded the right side (left-first). The opposite (right-first) was true in the other half. Half-face stimuli were presented unilaterally with the innermost edge aligned with the vertical meridian of the visual field. In place of the complementary half face, half of the mask stimulus was presented.

### 3.1.3. Data analysis

Accuracy indexes, laterality indexes, and mean RTs for correct matches of chimeric, entire, or half faces were calculated at each SOA, separately for left-first and right-first conditions. Trials with RTs less than 1000 ms (3.6%) and greater than 5000 ms (4.9%) were considered as anticipations and retards, respectively. Analyses were carried out as in Experiment 1. According to the assumption that the two cerebral hemispheres process information independently [13], the probability of a correct response on bilateral trials should be predicted by independently combining the probability of a correct response on left-half faces and on right-half faces presented alone. Combining the accuracy indexes for matching left- and right-half faces produces the following equation:  $AI_B = (AI_L + AI_R) - (AI_L \times AI_R)$ , where  $AI_B$  is the predicted bilateral accuracy index,  $AI_L$  the accuracy index for the left-half faces, and  $AI_R$  the accuracy index for the right-half faces. Thus, accuracy indexes in matching chimeric and entire faces were compared with the index of bilateral accuracy derived from analysis of responses to half faces.

## 3.2. Results

No participant overtly detected the presence of chimeric faces at 10, 20, and 30 ms SOA. Detection of conflicts occurred at 40 ms SOA for 2 participants, at 50 ms SOA for 9, and at 100 ms SOA for 7 participants. The remaining 4 participants did not consciously detect the presence of chimeric faces with SOAs up to 100 ms. In the blocks of trials following the conscious detection of conflicts, correct detection of chimeric faces occurred in 74.79% (SE = 8.66) of the trials in the left-first condition and in 76.62% (SE = 7.37) in the right-first condition [ $t(13) = -.51, P = 0.62$ ]. Data from blocks at 10, 20, 30, and 40 ms SOA, where the presence of chimeric stimuli went undetected, were entered

in the ANOVA. The 2 individuals who detected conflict at 40 ms SOA were not considered in the analysis. Thus, data from 20 participants were analyzed.

### 3.2.1. Accuracy index

Accuracy indexes for chimeric and entire faces and the predicted bilateral accuracy indexes derived from half-face trials were entered in an ANOVA with responding hand (left, right) as between-subjects variable and with the following within-subjects variables: type of stimulus (chimeric faces, entire faces, predicted accuracy), precedence (left-first, right-first), and SOA (10, 20, 30, 40 ms). Type of stimulus was significant [ $F(2,36) = 26.58, P < 0.001$ ], since accuracy was lower for chimeric (58.81%) than for entire faces (74.77%,  $P < 0.001$ ) and for predicted bilateral accuracy index (73.85%,  $P < 0.001$ ). SOA was also significant [ $F(3,54) = 20.93, P < 0.001$ ], since performance at 10 ms SOA (49.37%) was significantly lower than performance at 20 (75.22%), 30 (77.65%), and 40 ms SOA (74.35%). Precedence [ $F(1,18) = 0.85, P = 0.37$ ], responding hand [ $F(1,18) = 1.16, P = 0.296$ ], and interactions did not reach statistical significance.

### 3.2.2. RTs

RTs for chimeric faces, entire faces, and half faces were entered in an ANOVA with responding hand as between-subjects variable and with the following within-subjects variables: precedence, type of stimulus (chimeric faces, entire faces, half faces), and SOA. Among the main effects, precedence was marginally significant [ $F(1,18) = 4.15, P < 0.056$ ], since participants were faster in the right-first (1981.9 ms) than in the left-first condition (2034.66 ms). Type of stimulus was significant [ $F(2,36) = 21.38, P < 0.001$ ], because latencies were significantly higher for chimeric (2125.78 ms) than for entire faces (1867.23 ms,  $P < 0.001$ ) and half faces (2031.83 ms,  $P = 0.025$ ). Latencies for entire faces were significantly faster than for half faces ( $P < 0.001$ ). SOA was significant [ $F(3,54) = 28.12, P < 0.001$ ], since RTs at 10 ms SOA (2339.88 ms) were significantly slower than at 20 ms (2006.52 ms,  $P < 0.001$ ), 30 ms (1851.87 ms,  $P < 0.001$ ), and 40 ms SOA (1834.86 ms,  $P < 0.001$ ). Moreover, RTs at 20 ms SOA were higher than those at 30 ( $P = 0.017$ ) and 40 ms ( $P = 0.022$ ) SOA. The significance of the interaction type of stimulus  $\times$  SOA [ $F(6,108) = 2.45, P = 0.029$ ] is explained as follows: RTs to chimeric faces were significantly slower than those to entire faces at 10 ms SOA (2569.82 vs. 2132.86 ms,  $P < 0.001$ ) and at 20 ms SOA (2130.31 vs. 1834.03 ms,  $P = 0.001$ ). RTs to half faces were significantly slower than to entire faces at SOAs of 10 ms (2316.95 vs. 2132.86 ms,  $P = 0.008$ ) and 20 ms (2055.22 vs. 1834.03 ms,  $P = 0.02$ ). Half faces significantly differed from chimeric faces only at 10 ms SOA ( $P < 0.001$ ). No other effect resulted significant. Following the marginal significance of the main effect of precedence from the 4-way ANOVA, three separate repeated-measures ANOVAs were run for chimeric, entire,

and half faces, with precedence and ET as within-subjects variables. For chimeric faces, the main effect of precedence [ $F(1,19) = 9.57, P = 0.006$ ; Fig. 5] and ET [ $F(3,57) = 31.52, P < 0.001$ ] were highly significant. By contrast, the effect of precedence was not significant [ $F(1, 19) < 1$ ; Fig. 5] and only a significant main effect of ET resulted for entire [ $F(3,57) = 11.57, P < 0.001$ ] and half faces [ $F(3,57) = 8.57, P < 0.001$ ].

### 3.2.3. Laterality index

Laterality indexes for each SOA and in the two different precedence conditions are reported in Table 2. Values significantly higher than 50% (no side preference) indicate a preference towards the LHS (an effect which can be attributed to the RH dominance in processing unfamiliar faces). Inspection of Table 2 shows that, although significantly more probe stimuli corresponding to the RHS were chosen in the left-first condition, a strong tendency to choose probe stimuli corresponding to the LHS was observed in the right-first condition. Thus, the effect of precedence caused a partial reversal of cerebral dominance. In order to evaluate the extent of this reversal in cerebral dominance, we compared at each SOA the percentage of LHS matches in the right-first condition (laterality indexes in the right-first condition) with the percentage of RHS matches in the left-first condition (100–laterality index in the left-first condition) by means of series of dependent-sample *t* test (two-tailed). The tendency to match the LHS in the right-first condition was significantly stronger than the tendency to match the RHS in the left-first condition at 20 (70.34% vs. 59.06%,  $P = 0.027$ ), 30 (77.87% vs. 64.22%,  $P = 0.013$ ), and 40 ms SOA (69.35% vs. 51.33%,  $P = 0.007$ ), but not at 10 ms SOA (47.71% vs. 56.32%,  $P = 0.164$ ). Indeed, at 10 ms SOA, no preference toward one of the two half faces emerged in either precedence condition (Table 2), probably because of the high rate of errors observed in the block that was performed first. Results

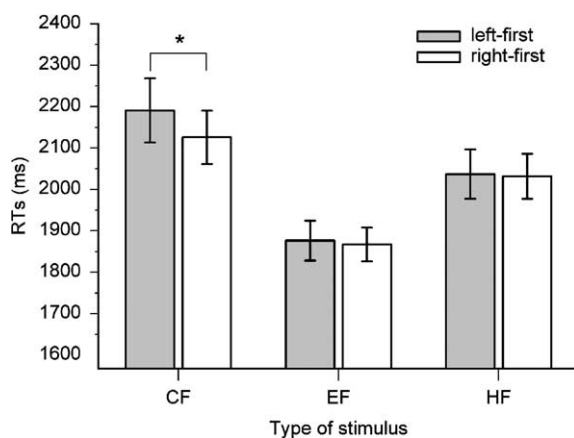


Fig. 5. Reaction times (RTs) in matching chimeric faces (CF), entire faces (EF), and half faces (HF) in Experiment 2. Means ( $\pm$ SE) are plotted separately for the left-first and the right-first precedence condition. Asterisk denotes significant comparison between the left-first and the right-first precedence conditions for each type of stimulus.

showed that the degree of the LHS-RH dominance in the right-first condition was significantly stronger than the degree of the RHS-LH dominance in the right-first condition. Thus, the extent to which the RH controlled the response when temporal cues favored its dominance was stronger than that of the LH when the right half faces were presented last.

An ANOVA with responding hand as between-subjects variable and precedence and SOA as within-subjects variables was performed on laterality indexes. The main effect of precedence was significant [ $F(1,18) = 96.82, P < 0.001$ ], because matches of the LHS were significantly more frequent in the right-first than in the left-first condition. SOA was significant [ $F(3,54) = 9.96, P < 0.001$ ], because laterality index was lower at 10 ms SOA than at the other asynchrony intervals (all  $P < 0.001$ ). A significant interaction precedence  $\times$  SOA was also observed [ $F(3,54) = 15.85, P < 0.001$ ], since matches of the LHS were significantly more frequent in the right-first than in the left-first condition at all SOAs ( $P < 0.001$ ) except 10 ms ( $P = 0.32$ ). The main effect of responding hand was not significant [ $F(1,18) < 1$ ], but the interaction of responding hand with precedence reached significance [ $F(3,54) = 5.94, P < 0.026$ ; Fig. 6]. Post hoc tests showed that matches of the LHS were significantly more frequent in the right-first than in the left-first condition. This was true both for participants responding with their left hand ( $P < 0.001$ ) and for participants responding with their right hand ( $P < 0.001$ ). The difference between the laterality indexes of the two groups was not significant in the right-first precedence condition ( $P = 0.129$ ); however, a nonsignificant tendency toward more LHS matches for the group responding with the right hand was observed in the left-first condition ( $P = 0.08$ ).

### 3.3. Discussion

Unlike Experiment 1 and previous studies using chimeric stimuli [29,36], in Experiment 2, the two halves forming chimeric- and entire-face target stimuli were presented asynchronously. The asynchronous presentation of the discrepant halves resulted in correct identification of chimeric stimuli for most participants. It is noteworthy that each half stimulus was presented for 30 ms, an ET at which all participants in Experiment 1 suppressed perceptual conflicts for simultaneous presentations. Suppression of conflicts occurred when the two halves were together on the screen, i.e., at 10 and 20 ms SOA, or when the disappearance of the first half was soon followed by the complementary one, i.e., at 30 ms SOA. The asynchrony that allowed most participants to become aware of the discrepancy in chimeric faces was 50 ms SOA or more. At 50 ms SOA, the interval between the disappearance of the first half and the appearance of the second half was 20 ms, which is the estimated interhemispheric callosal transfer of complex visual information [38].

Table 2

Laterality indexes for the left-first and the right-first conditions at each stimulus-onset asynchrony (SOA) in Experiment 2

| SOA (ms) | Left-first |     |          |    |          | Right-first |     |          |    |          |
|----------|------------|-----|----------|----|----------|-------------|-----|----------|----|----------|
|          | M (%)      | SE  | <i>t</i> | df | <i>P</i> | M (%)       | SE  | <i>t</i> | df | <i>P</i> |
| 10       | 43.7       | 4.2 | −1.51    | 19 | 0.147    | 47.7        | 3.6 | −.64     | 19 | 0.528    |
| 20       | 40.9       | 2.8 | −3.27    | 19 | 0.004    | 70.3        | 3.7 | 5.55     | 19 | 0.001    |
| 30       | 35.8       | 2.9 | −4.86    | 19 | 0.001    | 77.9        | 3.5 | 7.99     | 19 | 0.001    |
| 40       | 48.7       | 3.4 | −0.39    | 19 | 0.701    | 69.4        | 4.0 | 4.9      | 19 | 0.001    |

Note. Series of one-sample, two-tailed, *t* tests were carried out to assess significant divergence from 50% (a value where left matches equal right matches).

It is unlikely that practice effects per se account for the effect of SOA on detection of conflict. Indeed, Experiment 1 shows that participants failed to detect the presence of chimeric faces at 30 ms ETs independently from the ET order. Moreover, in Experiment 2, performance improved only between the first two blocks, namely, between 10 ms and 20 ms SOA. In contrast, no change was observed in the following blocks. The effect of asynchrony suggests that suppression of conflict is strictly related to the simultaneous presence of asymmetric figures in spatial locations where people usually expect to see somewhat symmetric stimuli, for example, faces.

Performance on chimeric faces was poorer than performance on entire or half faces. Interestingly, the presence of conflicting information impaired accuracy also with respect to the estimated performance of two independent hemispheres. The asynchronous presentation of the two halves forming chimeric faces induced better processing of the half face presented last. In particular, before the conscious detection of perceptual conflicts, participants showed a preference for the probe stimulus corresponding to the half stimulus presented last. The same reversal of cerebral dominance was observed no matter whether participants used their left or right hand. This effect suggests that

peripheral factors did not affect interhemispheric interaction in the present task. The preference to complete the half stimulus presented last induced a partial reversal of the typical RH dominance in face processing according to which the LHS should be matched independently from its position in the sequence. However, the effect of precedence cannot fully explain the pattern of results. The RH dominance when the LHS was presented last was stronger than the LH dominance when the RHS was presented last. Temporal cues interacted with the typical RH dominance in face processing, with a summation of effects when the last presented half was the one that is matched more frequently also under conditions of synchronous presentations. By contrast, when temporal cues favored the LH (which resulted non-dominant in face processing tasks under conditions of synchronous presentations), the effect of precedence was reduced. Temporal cues, however, were strong enough to induce a partial reversal of cerebral dominance.

This reversal of cerebral dominance is not explained by a shift in hemispheric specialization. Indeed, speed in matching chimeric faces was higher in the right-first condition, when an LHS-RH preference was found, than in the left-first condition, when an RHS-LH preference emerged. This pattern of results reflects the superiority of the RH in the face matching task, no matter which hemisphere holds sway of the response. Thus, results hint at a reversal of typical hemispheric dominance but not of hemispheric specialization when left-sided stimuli are presented first.

#### 4. General discussion

Interhemispheric interaction and interhemispheric competition in handling information from the environment and in producing integrated behavioral responses have been studied in both split-brain and intact individuals [8,11,15]. The asynchronous stimulation of the two cerebral hemispheres and the presentation of chimeric faces at different ETs allowed investigating interhemispheric interaction and metacontrol in healthy individuals.

No participant was able to consciously detect the conflicting information carried by the chimeric faces for simultaneous presentation lasting up to 40 ms. In fact, for several participants in Experiment 1, the presence of chimeric faces went undetected even at 90 ms ET. Within

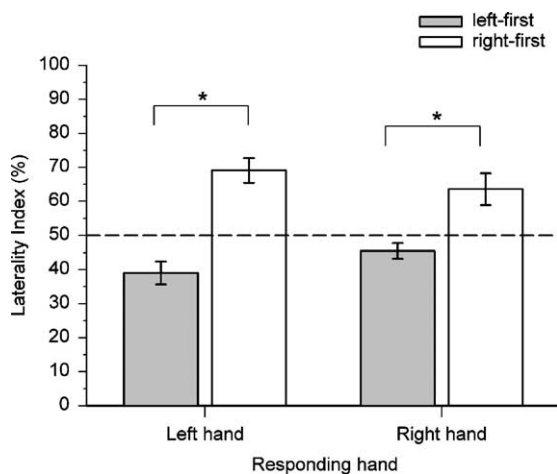


Fig. 6. Laterality indexes in matching chimeric faces in Experiment 2. Means ( $\pm$ SE) are plotted according to precedence condition and responding hand. Values of 50% indicate that left choices were identical to right choices. Values higher than 50% indicate that more left-half stimuli were matched, whereas values lower than 50% indicate that more right-half stimuli were matched. Asterisks denote significant comparison between the left-first and the right-first precedence conditions for each group.

this ET window, participants completed one of the halves forming the chimeric faces, so that a unitary conscious percept resulted. Thus, the brief ET prevented the two cerebral hemispheres from integrating their visual images and consequently the healthy individuals behaved as though their corpus callosum was not functioning. In the present study, suppression of conflicts was found using chimeric half stimuli directly abutting along the vertical midline of the visual field and thus stimulating the two loci of the primary visual cortices that are cross connected via the corpus callosum [16]. This may seem at odds with respect to previous studies in which suppression of conflict occurred only when the junction of chimeric stimuli was covered [29,44]. Milner and Dunne [29], for example, found that covering the junction line did not allow healthy individuals to detect chimeric stimuli presented for 100 ms. It is important to note that most participants of our study could clearly see the discrepancy in chimeric faces for presentations lasting less than 90 ms. This result may suggest that interhemispheric integration of stimuli with higher eccentricity requires more time.

Once the presence of chimeric stimuli was overtly detected, participants were able to distinguish chimeric from entire faces, thus hinting at a role of expectation of symmetric faces in the suppression of conflicts. The suppression of conflict observed in this study may allow the maintenance of a unitary consciousness of the world under conditions of uncertainty. Once the perceiver knows that discrepant stimuli can be presented, the suppression mechanism loses its functional role and the perceptual conflict can be accurately perceived at a conscious level. Notably, merging incongruent features into a unitary percept occurred only when the two halves of chimeric faces were simultaneously presented to the two hemispheres. Under conditions of asynchronous presentation, each hemisphere independently carries out its early visual encoding and perceptual processing of information. Thus, awareness of perceptual conflicts may be linked to the time available for comparing the percepts of the hemisphere stimulated first and of that stimulated last. This effect suggests that suppression of conflicts and completion are strictly related to the simultaneous presence of the two stimuli in the visual space.

We tachistoscopically presented the two half faces compounding chimerics in the two half visual fields; interhemispheric interaction was, thus, required to integrate the conflictual stimuli. The present data, however, cannot tell apart whether or not suppression of perceptual conflicts only occurs when interhemispheric interaction is required. It may be that conflictual information in chimeric faces is suppressed also when the two half faces are presented to the same hemisphere. Indeed, suppression of conflicts in chimeric faces may reflect the binding of object parts or features into a unitary percept across spatial and temporal discontinuities [39]. Psychophysical studies clearly demonstrated perceptual binding difficulties under condition of

brief exposures or non-focused attention [39,41]. Moreover, when objects are partially occluded, the visual system rapidly completes the objects by filling in the missing information [33]. Several factors, like temporal or spatial contingencies, may determine whether or not different parts or features will be bound together [40]. For example, Leonards et al. [21] presented participants with a texture segmentation paradigm. Texture patterns were defined by line orientation and/or by phase asynchrony, which could be reciprocally congruent or incongruent. Both orientation and phase asynchronies, when exceeding the 10 ms interval, could be used to segment textures when the two cues were congruent. However, conflicting temporal cues, up to phase intervals of 100 ms, did not interfere with the texture-defined pattern, thus showing that the visual system is tuned to compensate for the brief asynchronous temporal disruptions that may occur in the visual scene. The same mechanism may explain why merging incongruent features into a unitary percept in the present study occurred only when the two halves of chimeric faces were simultaneously presented to the two hemispheres. However, intra- and interhemispheric perceptual binding may have different temporal dynamics, in accordance with the different neural paths used to integrate information presented in the same or in different visual fields. Indeed, the strong influence of temporal asynchrony observed in Experiment 2 seems quite at odds with the nonsignificant effect of large temporal asynchronies on the perceptual salience of one of two identical and partially overlapping Kanizsa triangles formed by illusory contours [7]. In this type of stimuli, observers may perceive one of the two illusory figures alternating over time. That is, both triangles are equally likely to be perceived, but they are never perceived simultaneously. Small spatial displacements in the elements inducing illusory contours of one of the two triangles are strongly effective in favoring the other figure, whereas large asynchronies in the presentation of the elements inducing illusory contours are ineffective [7]. This result is in keeping with studies showing that temporal synchronicity has no effect on the probability of illusory conjunctions errors, that is, the attribution of the feature of one object to another (e.g., [20]). Thus, while temporal asynchrony seems to be ineffective in the intrahemispheric integration of information, it may play a crucial role in the interaction between the two cerebral hemispheres. Future studies are needed, however, to better understand the role of temporal cues in the intra- and interhemispheric integration of facial stimuli both in healthy and split-brain individuals. Moreover, a broader sample of stimuli should be used in order to verify whether or not suppression of conflictual information that is presented simultaneously in the visual scene is restricted to stimuli with a highly symmetric structure, like faces, where the two halves share most features.

Recently, suppression of conflicts in healthy individuals was also reported in a study where one half face was degraded [44]. Interestingly, the low-contrast half face did

not interfere with performance in matching the high-contrast half faces. Under these conditions, however, the lack of relevant information from one side more than the conflicts between half stimuli seems to account for the integration of half faces into a unitary percept. The stimuli used in our experiments clearly induced a conflict when the visual images projected to the two hemispheres were chimeric. Although unreported consciously, this conflict impaired accuracy and speed in matching chimeric faces with respect to entire or even half faces, for both simultaneous and asynchronous presentations. It is unlikely that low-level perceptual factors explain why participants did not detect the presence of chimeric faces. Indeed, suppression of conflicts occurred also at 40 ms ET, when participants' performance in matching chimeric and entire faces was good.

In principle, differences in processing chimeric and entire faces could also be linked to different matching strategies called into play with the two types of stimuli. Chimeric faces, for example, could have been matched by using an analytical strategy, and entire faces could have been matched by using a more holistic strategy [37]. As the second strategy leads to a better performance [37], the better performance on entire faces could be explained without calling into play an implicit processing of conflict. Performance improvement contingent upon the increase of ET, however, was parallel for chimeric and entire faces, suggesting that the same mechanism was employed for matching the two types of stimuli. The linear increase in accuracy suggests that participants learned to match each half of chimeric faces, even if they did not detect perceptual conflicts at a conscious level. That information arising from the processing of chimeric stimuli was able to implicitly induce behavioral changes is also supported by the observation that, at ETs where the presence of strange stimuli was not noticed, our participants screwed up their faces, smiled wryly, or frowned only during the presentation of chimeric faces. All this evidence suggests that perceptual conflicts were processed at an unconscious level, influencing cognitive and emotional performance.

The implicit processing of conflicts shown by healthy individuals recalls what was observed in brain-damaged patients with hemi-spatial neglect when they were presented with chimeric stimuli [5,31,32,42,43]. Although in brain-damaged patients the effects may be disclosed even when stimuli are presented under free-viewing conditions, our results suggest that very fast presentations of chimeric figures may allow investigating overt and covert information processing also in healthy individuals. Furthermore, as in studies of brain-damaged patients with neglect [32], chimeric stimuli can be useful for disentangling any selective influence of perceptual (low-level) and semantic or emotional (high-level) conflicts on interhemispheric interactions.

It is known that visual stimuli presented bilaterally are processed faster and more accurately than unilateral stimuli (bilateral advantage; see [6,19,26,30,34]). Studies in monkeys with intact commissures indicate that such a bilateral

advantage is lost when discrepant stimuli are presented concurrently to the two cerebral hemispheres [34]. The impairment in matching chimeric faces in our study is not simply due to the loss of the bilateral advantage, insofar as performance on chimeric stimuli was lower than the predicted bilateral accuracy of two independent hemispheres. That performance on entire faces was not better than the predicted bilateral accuracy of two independent hemispheres may be related to what Mohr et al. [30] reported. These authors found a bilateral advantage in matching familiar but not unfamiliar faces. Indeed, the face models used in our experiments were not familiar to the participants and it is unlikely that each experiment was long enough to induce familiarity.

Another novel result of the present study is that the precedence of hemispheric stimulation caused a shift in hemispheric dominance, insofar as the hemisphere stimulated last appeared to influence the response. This recency effect may be due to a backward masking of the second on the first half face. Several studies reported that perception of a target may be disrupted by the appearance of another object in a proximal spatial location (metacontrast masking; for a review, see [3]). It is noteworthy, however, that the two half faces were presented tachistoscopically in different visual half fields, each projecting to the contralateral hemisphere. Thus, the interference between the two half faces likely occurred at late cortical levels, following the interhemispheric transfer of information. Recency, however, cannot fully explain the pattern of results observed in Experiment 2. Indeed, the advantage of the last presented half faces was not symmetric in the two half fields, because the tendency to match the left half faces, when it was presented last, was stronger and more stable than the tendency to match the right half faces when it was presented last. The effect of recency, thus, interacted with the typical RH dominance in face processing by inducing a partial reversal of the hemisphere that tended to assume control of response. This result suggests that cerebral dominance is not fixed, but it may be influenced by dynamic factors, like the timing of hemispheric stimulation. This reversal of cerebral dominance, however, was not caused by a shift in hemispheric specialization. Thus, a dissociation between hemispheric dominance and specialization emerged in our study.

In keeping with studies on split-brain [23,24] and healthy individuals [12,13], this result hints at the existence of the hemispheric metacontrol. The previous finding of hemispheric metacontrol in healthy individuals [12,13] was obtained by inducing a conflict between the strategies employed by the two cerebral hemispheres in processing the same, redundant stimulus information. In our study, a more striking perceptual conflict in hemispheric stimulation was created and a dissociation between hemispheric specialization and dominance was found. Thus, metacontrol is not merely an abnormality of the split-brain condition, but it likely represents a very important operational mechanism in normal interhemispheric interactions.

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