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Functional asymmetry and interhemispheric cooperation in the perception of emotions from facial expressions

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Abstract The present study used the redundant target paradigm on healthy subjects to investigate functional hemispheric asymmetries and interhemispheric cooperation in the perception of emotions from faces. In Experiment 1 participants responded to checkerboards presented either unilaterally to the left (LVF) or right visual half field (RVF), or simultaneously to both hemifields (BVF), while performing a pointing task for the control of eye movements. As previously reported (Miniussi et al. in *J Cogn Neurosci* 10:216–230, 1998), redundant stimulation led to shorter latencies for stimulus detection (bilateral gain or redundant target effect, RTE) that exceeded the limit for a probabilistic interpretation, thereby validating the pointing procedure and supporting interhemispheric cooperation. In Experiment 2 the same pointing procedure was used in a go/no-go task requiring subjects to respond when seeing a target emotional expression (happy or fearful, counterbalanced between blocks). Faster reaction times to unilateral LVF than RVF emotions, regardless of valence, indicate that the perception of positive and negative emotional faces is lateralized toward the right hemisphere. Simultaneous presentation of two congruent emotional faces, either happy or fearful, produced an RTE that cannot be explained by probability summation and suggests inter-

hemispheric cooperation and neural summation. No such effect was present with BVF incongruent facial expressions. In Experiment 3 we studied whether the RTE for emotional faces depends on the physical identity between BVF stimuli, and we set a second BVF congruent condition in which there was only emotional but not physical or gender identity between stimuli (i.e. two different faces expressing the same emotion). The RTE and interhemispheric cooperation were present also in this second BVF congruent condition. This shows that emotional congruency is the sufficient condition for the RTE to take place in the intact brain and that the cerebral hemispheres can interact in spite of physical differences between stimuli.

Keywords Emotion · Hemispheric asymmetry · Bilateral gain · Interhemispheric interaction · Redundant target effect · Face perception

Introduction

The left (LH) and right (RH) cerebral hemispheres constitute two subsystems of a more general and highly integrated information processing system. Notwithstanding the unified stream of consciousness that people experience in everyday life, there is compelling evidence that the cerebral hemispheres show functional specialization in a number of perceptual, cognitive, and motor tasks (Hellige 1993). For instance, language processing appears to be lateralized in the LH (Sperry et al. 1969), whereas visuospatial cognition is more often related to the RH (Davidson and Hugdahl 1995). Although such functional hemispheric asymmetries seem to apply also to the processing of facial expressions, the details are still under debate. Specifically, the principle according to which the perception of emotions from faces is lateralized in the human brain is still not clear (Davidson 1993; Gainotti 2000). Indeed, the somewhat contradictory results in the literature can be grouped in two main contrasting theories: the right-

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hemisphere hypothesis as opposed to the valence hypothesis. The former hypothesis posits that the RH is specialized for processing emotions (either positive or negative), whereas the latter assumes that positive emotions are preferentially processed by the LH and negative emotions by the RH (Borod et al. 1998; Canli 1999 for a review). To date, there are data supporting both the right-hemisphere and the valence hypotheses, and recently some authors have also put forward new hybrid models incorporating aspects of these two theories (Adolphs et al. 2001; Davidson 1995; Gainotti 2001).

A directly related issue concerns the nature, absolute or relative, of this functional lateralization. Early neurological models tended to conceive cognitive and emotional functions as localized only in one hemisphere and, consequently, spoke of absolute hemispheric *dominance* (Jackson 1874, 1880; Mills 1912a, b; Gainotti 1972, 1984). In contrast, more recent studies have challenged this view and have emphasized the notion of relative, instead of absolute, hemispheric specialization even for markedly lateralized functions (e.g., language) (Gazzaniga 2000; Pulvermüller and Mohr 1996; Schweinberger et al. 1994). This leads to the question of interhemispheric interaction; that is, how, to what extent, and under which conditions the cerebral hemispheres cooperate and coordinate their respective processing abilities to operate more efficiently (Hoptman and Davidson 1994).

The redundant target paradigm (RTP) provides a solid and theoretically founded methodology for testing functional specialization and interhemispheric cooperation with behavioural measures in visuo-perceptive tasks. In its general form, this procedure consists in the tachistoscopic presentation of visual stimuli either unilaterally to the left (LVF) or to the right visual half-field (RVF), or simultaneously to both hemifields (BVF) and requires subjects to perform a detection or a more demanding decision task (Dimond and Beaumont 1972). The anatomy of the primary visual pathways is such that LVF and RVF stimuli project to the RH and LH, respectively. Thus, by comparing performance differences (in terms of latency and/or accuracy) between the two unilateral conditions, it is possible to examine functional hemispheric asymmetries. In addition, the absolute or relative nature of the hemispheric specializations can be assessed by contrasting the performance in the *best* unilateral condition with the performance in the condition of bilateral stimulation. Indeed, since the absolute dominance interpretation postulates that only one hemisphere is in charge of a particular cognitive function, the same standard in performance is expected irrespectively of whether the dominant or both hemispheres are stimulated. Conversely, a relative functional asymmetry model would predict better processing in the bilateral condition as compared to the best unilateral condition (bilateral gain or redundant target effect, RTE) (Zaidel and Rayman 1994).

Observations of bilateral gain were used in support of interhemispheric cooperation but further analysis is needed before alternative explanations can be ruled out (Miller 1982, 1986). Indeed, this effect, while providing clear evidence on the relative nature of hemispheric specialization, does not necessarily imply that the two hemispheres cooperate to accomplish the task. Separate-activation or race models account for a bilateral gain simply relying on the fact that the probability of fast detection increases with the number of targets (Raab 1962; Townsend and Ashby 1983). These models consider the two hemispheres as two independent and parallel processing systems where the information is never combined across perceptual channels and only one target is directly responsible for the observed response also on bilateral trials. Hence, the RTE is explained in terms of probability summation or statistical facilitation: if the time required for a target to trigger a response varies stochastically across trials, the average finishing time for the faster of two parallel processes will be shorter than the average response time for either process alone. In contrast, coactivation models assume the presence of a functional interaction between the perceptual channels at some level along the information processing stages that results in a reduction of response time (Colonius 1986, 1988; Miller 1982, 1986; Schwartz 1989; Ulrich and Giray 1986). Multiple stimuli are summed in an activation pool before reaching the threshold for response execution, so that in bilateral trials it is possible for both targets to be partially responsible for the observed response. Clearly, with two targets contributing activation toward the same threshold, the response is activated more rapidly than when there is only one target contributing activation. Although the concept of coactivation originally proposed by Miller (1982, 1986) was not necessarily linked to neural activity, several more recent studies on brain-damaged patients and with neuroimaging techniques have argued convincingly that it is equivalent of neural summation and interhemispheric interaction (Corballis 1998; Corballis et al. 2002, 2003; Iacoboni et al. 2000; Iacoboni and Zaidel 2003; Marzi et al. 1996; Miniussi et al. 1998; Reuter-Lorenz et al. 1994; Roser and Corballis 2002, 2003; Savazzi and Marzi 2002).

Most of the previous behavioural studies reported a bilateral gain in healthy and brain-damaged subjects, for various types of stimuli, and in different tasks (mainly simple reaction time and go/no-go tasks). For instance, the RTE has been shown using simple flashes (Corballis 2002; Savazzi and Marzi 2002), checkerboards (Miniussi et al. 1998), shapes and colours (Mordkoff and Yantis 1993), letters (Grice and Reed 1992; Mordkoff and Miller 1993), and letterstrings (Marks and Hellige 1999), on healthy subjects as well as on neurological patients (with hemianopia and blindsight: de Gelder et al. 2001; Marzi et al. 1986; hemispherectomy: Tomaiuolo et al. 1997; split-brain: Corballis 1995; Forster and Corballis 2000; Iacoboni et al. 2000; Mohr et al. 1994; Reuter-Lorenz et al. 1994;

Roser and Corballis 2002, 2003; and visual extinction: Marzi et al. 1996). In normal viewers the RTE has also been demonstrated with meaningful stimuli such as words (Hasbrooke and Chiarello 1998; Mohr et al. 1996), numbers (Ratinckx and Brysbaert 2002), drawings of animals or objects (Koivisto 2000), and familiar neutral faces (Mohr et al. 2002). Likewise, direct tests have often shown violations or race models, thereby providing support for models based on neural coactivation and interhemispheric summation (Corballis 2002; Grice and Reed 1992; Iacoboni et al. 2000; Iacoboni and Zaidel 2003; Marzi et al. 1996; Miller 1982, 1986; Miniussi et al. 1998; Mordkoff and Yantis 1993; Reuter-Lorenz et al. 1994; Savazzi and Marzi 2002).

To our knowledge, only two recent studies have used the RTP with emotional facial expressions, yielding conflicting results. de Gelder et al. (2001, Experiment 3) reported faster reaction times with two congruent facial expressions than with the unilateral presentation of the same faces in the intact LVF of a patient with hemianopia but limited residual vision (blindsight). This led us to the prediction that normal viewers might also show a bilateral advantage for emotional faces. Yet Schweinberger et al. (2003, Experiment 2) reported a somewhat paradoxical and contrasting finding, failing to show any bilateral gain with emotional faces on normal subjects in a two-choice reaction time task and, hence, suggesting a detrimental role for conscious perception and/or attention with affective stimuli. Furthermore, the authors observed no significant difference in response latency between unilateral left and right conditions, which is a challenge for both the valence and the right-hemisphere hypothesis on functional asymmetry for the perception of facial expressions. Finally, a direct contrast between race and coactivation models has never been investigated with emotional faces, leaving uncertainties about whether the cerebral hemispheres interact in such a task.

In the present study we took advantage of the RTP in order to test for the functional specialization and the interhemispheric cooperation in processing emotional faces on normal subjects. The first experiment was a replication of previous studies reporting a response gain in latencies with simple stimuli (checkerboards) when healthy (Miniussi et al. 1998) and brain damaged subjects (de Gelder et al. 2001, Experiment 1) are required to perform a detection task. Our aim was to test the reliability of a pointing procedure that allows a stringent control of eye movements. The validation of the pointing procedure provided by evidence of normal RTE would set the stage for the second and third experiments that investigated: (a) how the perception of emotions from faces is lateralized in the intact brain, (b) the nature, absolute or relative, of this functional specialization, (c) the existence of interhemispheric cooperation (Experiment 2); and (d) whether the RTE and the neural summation for emotional faces occur also when the stimuli are emotionally congruent but physically different (Experiment 3).

Experiment 1

Method

Participants

Twenty-two healthy volunteers (18 women) contributed data for this experiment ($M = 25.13$ years, $SD = 3.52$, age range = 19–32). All participants reported normal or corrected-to-normal visual acuity and no history of neurological or psychiatric illness. The majority of the participants composing our sample were right-handed as assessed by the Edinburgh handedness inventory ($M = 65.88$, $SD = 23.9$) (Oldfield 1971). The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and participants provided written informed consent approved by the Ethical Committee of the University of Turin, Italy.

Stimuli and apparatus

The stimuli consisted of rectangular black-and-white checkerboards (7×11 cm) sustaining a visual angle of $\sim 10^\circ$ horizontally and $\sim 15.45^\circ$ vertically from a viewing distance of ~ 40 cm. The rectangles were centred vertically and the innermost edge was placed 11 cm to the right or left of the central fixation cross corresponding to $\sim 15.45^\circ$ of eccentricity. Mean stimulus luminance was 38 cd/m^2 and mean luminance of the white background was 85 cd/m^2 . The stimuli were presented for 200 ms either singly in the LVF, in the RVF, or simultaneously in BVF on a 21-inch Elo Touch CRT monitor (vertical refresh = 85 Hz, dot pitch = 0.28, SD of positional accuracy error < 2.03 mm, touch activation force < 85 gr). The monitor was connected to an IBM-compatible Pentium PC that controlled stimulus presentation and data recording by means of SuperLab 2.0 software (Cedrus Corporation).

Procedure

Participants were tested in a dimly lit room during an experimental session lasting approximately 1 h. They were seated at the reaching distance of ~ 40 cm from the monitor, the vertical midline of which lay on the sagittal midplane of their trunk and head. Each trial started when the subjects reached for the central fixation cross and pressed it with their forefinger. The size of the central cross ($\sim 1.25^\circ$) required visual fixation during the reaching phase, so that the two halves of the screen fell into the corresponding halves of the subject's visual field (Bisiach et al. 1989). On regular trials, pressing the cross was immediately followed either by unilateral LVF, RVF, or BVF stimuli. On catch trials no stimuli were presented, or were presented with an unpredictable delay of 800 or 1,200 ms. In the delayed catch trials, unilateral

LVF stimuli appeared in 1/3 of the repetitions, unilateral RVF stimuli appeared in another 1/3, and BVF stimuli were presented in the remaining 1/3 of the repetitions for each of the two delays. Participants signalled the detection of the stimuli, regardless of their position or number, by pressing a vertically oriented key at the bottom of the screen via a ballistic movement with the same hand used for pressing the central cross. Catch trials were introduced to discourage the participants from responding automatically after the pointing task rather than to the actual presence of the stimuli. These trials were then discarded from analyses. The subjects were instructed to respond as fast and as accurately as possible (Fig. 1).

Before starting the experiment a practice block of 45 regular trials (15 trials per condition; i.e. LVF, RVF, and BVF) and 24 catch trials was run. The experiment consisted of four blocks. Each block comprised 90 randomized regular trials (30 repetitions each for LVF, RVF, and BVF conditions) and 45 catch trials (15 repetitions each for no stimuli, 800 ms, and 1,200 ms delay). Participants were thus presented with a total of 120 repetitions for each type of stimulus condition (LVF, RVF, and BVF) and 60 repetitions for each type of catch trial (no stimuli, 800 ms, and 1,200 ms delay). Response hand was balanced between blocks. Half of the subjects started with the right hand, half with the left, changing hand after each block.

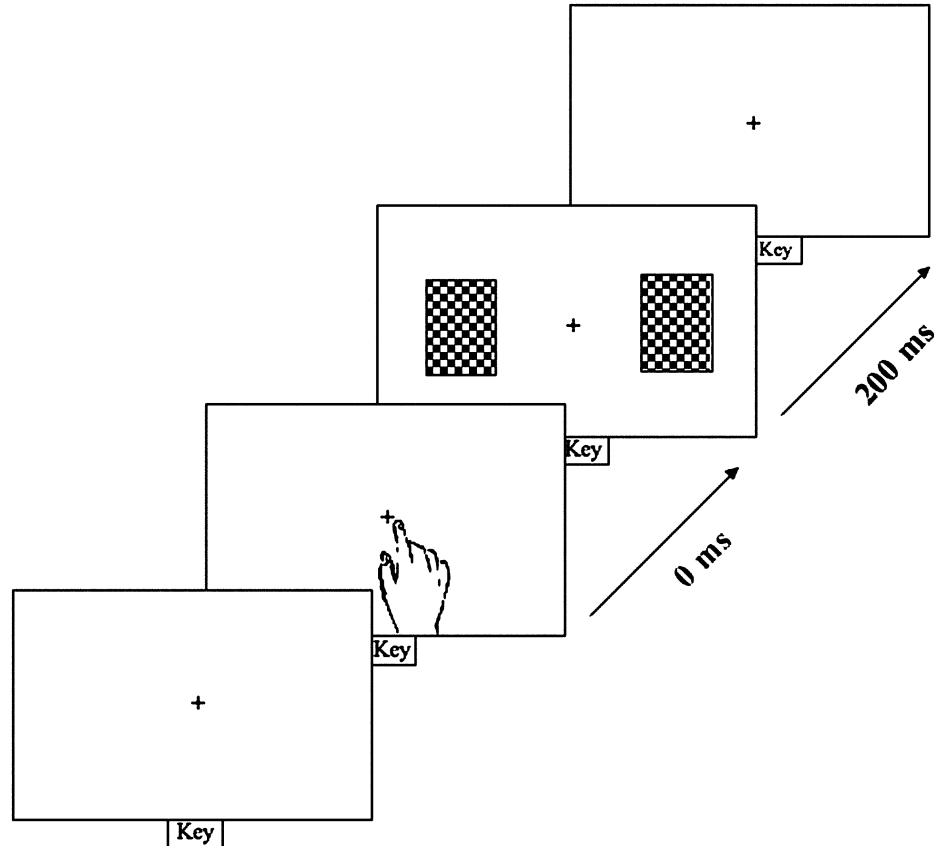
Data analysis

RTE assessment

Latencies and response accuracy to regular trials were analysed. A 2×3 repeated-measures ANOVA was conducted separately on mean reaction times (RTs) for correct responses and errors with two within-subjects factors: response hand (left vs. right) and stimulus condition (LVF, RVF, and BVF). Responses faster than 200 ms and slower than 1,000 ms were, respectively, considered as anticipations and delays, and were removed from statistical analysis. Post hoc Scheffé test was chosen to further analyse significant main effects and interactions.

Since analyses of RTs based on mean values may lead to spurious findings (Ratcliff 1979), we plotted the complete cumulative distribution function (CDF) of RTs in each of the three conditions of stimulus presentation. To obtain these CDFs, we first rank-ordered RTs in each subject and for each stimulus type. Specific values for the CDFs were calculated at 1% steps from the 1st to the 99th percentile, thereby estimating the RTs at each percentile of the true CDFs. Composite CDFs for each condition were then obtained simply by averaging across subjects all the RTs at each percentile. This detailed graphical description of the RT distributions provides additional support to the evidence of RTE

Fig. 1 Procedure used in Experiment 1 in a regular trial with bilateral stimuli



obtained by summary statistics on the mean values and requires that RTs in the bilateral condition should be faster than those of the unilateral conditions throughout the whole distribution. The significance of the differences between bilateral and unilateral CDFs was tested with paired-sample t tests carried out at each percentile of the distributions.

Evaluation of the interhemispheric cooperation

To distinguish between probabilistic and neural coactivation explanations of the bilateral gain we adopted the approach suggested by Miller (1982, 1986). The race-model inequality test of Miller is based on CDFs for RTs and sets an upper limit on the facilitation produced by bilateral stimuli for any time t assuming separate activation:

$$P(\text{RT} \leq t | S_L \text{ and } S_R) \leq P(\text{RT} \leq t | S_L) + P(\text{RT} \leq t | S_R),$$

where $P(\text{RT} \leq t | S_L \text{ and } S_R)$ is the cumulative probability of a correct detection with bilateral stimuli, $P(\text{RT} \leq t | S_L)$ is the cumulative probability of a response given one target in the LVF and nothing in the RVF, and $P(\text{RT} \leq t | S_R)$ is the cumulative probability of a response given one target in the RVF and nothing in the LVF. Consistently, since separate activation or race models predict no interaction between channels (hemispheres), the probability of responding to redundant stimuli by time t must not be higher than the sum of the probabilities associated to either unilateral stimuli. Thus, the violation of the inequality indicates a bilateral gain that exceeds the upper limit of probability summation and is inconsistent with any race model, thereby supporting an interpretation in terms of neural summation and interhemispheric cooperation. Conversely, given the very conservative nature of this test, even when the race model inequality is not violated, it cannot be excluded that the facilitation observed in the bilateral condition is due to neural summation. To test for the reliability of the race model violation we performed a

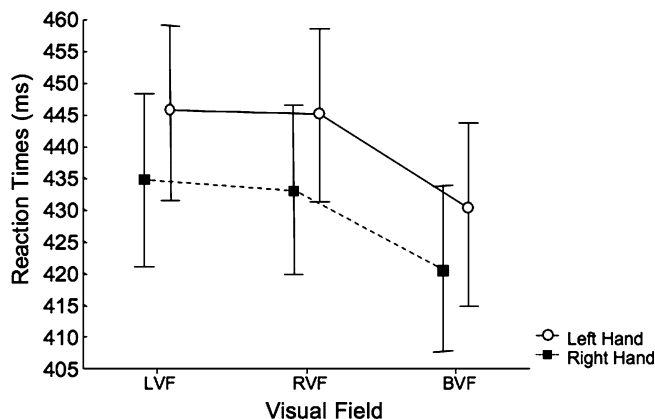


Fig. 2 Mean RT and standard error (SE) as a function of response hand for LVF, RVF, and BVF conditions. LVF left visual field, RVF right visual field, BVF bilateral visual field

series of paired-sample t tests at each percentile of the CDFs in which a violation occurred descriptively. It is worth noting that the inequality can be violated only when the value of t is relatively small. Indeed, as t gets larger, the left side of the equation goes to a maximum of one while the right side goes to a maximum of two. Therefore, empirical tests of the inequality must focus on small values of t and, in any case, on values of t such that $P(\text{RT} \leq t | S_L) + P(\text{RT} \leq t | S_R) \leq 1$.

Results

Latency and accuracy analysis

Overall, participants responded faster to bilateral ($M = 425$ ms; $SD = 63$) than to unilateral stimuli (LVF: $M = 440$ ms, $SD = 63$; RVF: $M = 439$ ms, $SD = 63$) irrespectively of the response hand used (Fig. 2).

The ANOVA on mean RTs confirmed this observation revealing a significant main effect of stimulus condition [$F(2,42) = 37.4$, $P < 0.0001$], no significant effect of response hand, and no significant interaction between these two factors. Post hoc tests showed that the contrasts between the bilateral and the unilateral left and right conditions were both significant (BVF vs. LVF, $P < 0.0001$; BVF vs. RVF, $P < 0.0001$). The difference between the two unilateral conditions was not significant ($P = 0.82$).

It is evident from Fig. 3 that the RTs in the bilateral condition were consistently faster than those of the unilateral conditions throughout the whole distribution. These differences were statistically significant from the 1st to the 77th percentile in the comparison between BVF and LVF conditions [$t(21) \geq 1.75$, $P \leq 0.048$] and from the 1st to the 76th percentile in the comparison between BVF and RVF conditions [$t(21) \geq 2.77$, $P \leq 0.006$], which provides convincing evidence for the reliability of the RTE.

The percentages of misses for LVF, RVF, and BVF conditions were, respectively, 0.57, 0.64, and 0.34% when responding with the left hand, and 0.61, 0.46, and 0.49% when using the right hand. The ANOVA on mean errors showed no significant effect of response hand [$F(1,21) = 0.000$, $P = 1$], stimulus condition [$F(2,42) = 1.208$, $P = 0.309$], and no significant interaction [$F(2,42) = 0.741$, $P = 0.48$], thus ruling out any interpretation in terms of speed/accuracy trade-off.

No subject reacted wrongly to catch trials without stimuli.

Evidence for interhemispheric cooperation

We compared the CDFs for bilateral targets with the sum of the corresponding CDFs for unilateral left and right trials to determine whether the observed bilateral gain might be accounted for by probability or by neural summation.

Figure 4a shows the comparison represented in the inequality test. When the CDFs are plotted, race models

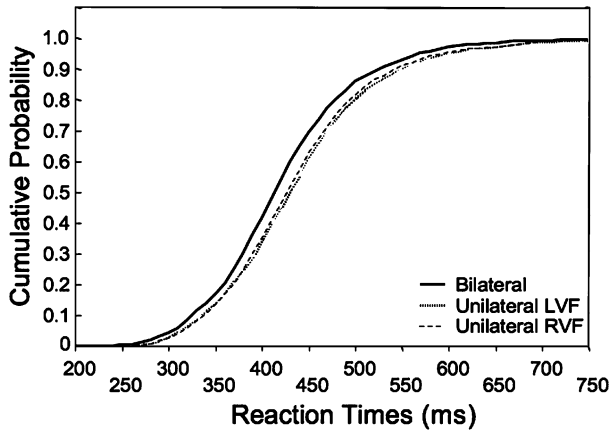
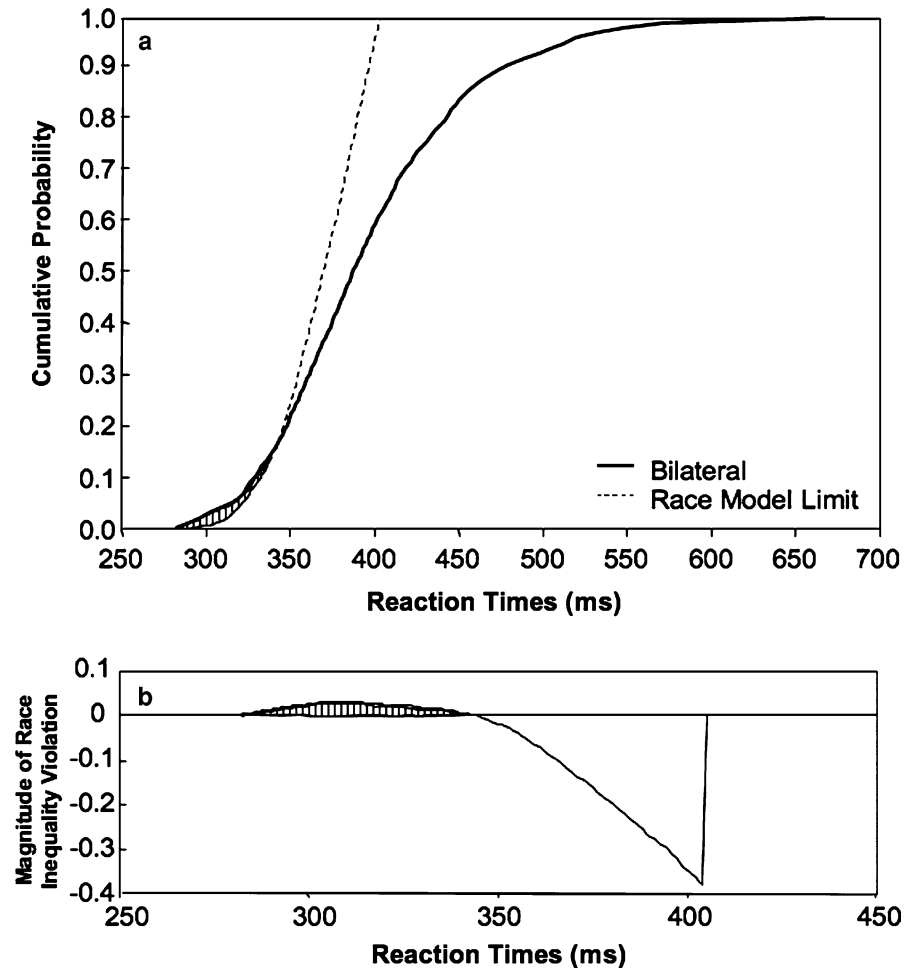


Fig. 3 Cumulative distribution functions (CDFs) of the mean RTs for LVF, RVF, and BVF conditions. Evidence of the RTE requires that RTs in the bilateral condition should be faster (i.e. represented above and to the left) than those of the unilateral conditions throughout the whole distribution

require that the CDF of bilateral trials be *everywhere* below and to the right of the summed CDF for unilateral trials. Conversely, violations of the upper limit of the race model are indicated *whenever* the probability associated with the bilateral CDF exceeds the sum of the unilateral

Fig. 4 Violation of the race model. Comparison represented in inequality test. **a** Observed CDF in the condition of bilateral presentation and the performance limit of the race model (sum of unilateral LVF and RVF CDFs). Violations of the race model are indicated by the vertical hatching. **b** Differences between the CDF for bilateral stimuli and the race model limit. Violations are indicated by positive values and the vertical hatching



CDFs. These violations, indicated in the figure by the vertical hatching, were statistically significant in the range 285–340 ms, corresponding to the estimates of the CDFs from the 1st to the 13th percentile [$t(21) \geq 2.07$, $P \leq 0.028$].

Figure 4b illustrates the difference between the bilateral CDF and the race inequality limit. Although the two representations are substantially equivalent, we will report the results in this last format since it is more informative to present the difference between the obtained and predicted CDFs.

Discussion

This experiment successfully replicates previous findings reporting a bilateral gain for similar visual stimuli in normal observers (Miniussi et al. 1998) and in hemianopic patients (de Gelder et al. 2001; Marzi et al. 1996). This clearly validates the pointing procedure adopted here. Indeed, while providing a careful check of eye movements, the pointing task did not interfere with the RTE. In keeping with the study by Miniussi et al. (1998), we observed no difference between unilateral conditions, indicating similar competences of both hemispheres in detection tasks with simple stimuli. Likewise, the RTE reported in the present experiment exceeded the limits

for a probabilistic interpretation, suggesting that neural summation and interhemispheric cooperation occurred in our sample.

Lastly, the RTE was present irrespectively of the hand used by subjects for providing responses. In fact, there was a generalized, but not significant, reduction in RTs when the right hand was used, as can be expected in a sample of right-handed subjects. Similarly, the use of either hand did not interact with the visual hemifield stimulated in the unilateral conditions, as we did not observe any stimulus-response compatibility effect (i.e. faster RTs when the visual hemifield stimulated and the response hand are controlled by the same hemisphere). This further supports the issue of interhemispheric interaction (Olk and Hartje 2001).

Experiment 2

Method

Participants

Twenty-five new volunteers (20 women) were enrolled in this second experiment ($M = 25.31$ years, $SD = 3.61$, age range = 19–32). They all reported normal or corrected-to-normal visual acuity and no history of neurological or psychiatric illness. All participants were right handed ($M = 66.12$, $SD = 24.2$) (Oldfield 1971).

Stimuli and apparatus

Twelve greyscale photographs from Ekman's series (Ekman and Friesen 1976) (four actors, two males and two females each with either a happy, fearful, or neutral expression) were presented for 200 ms in the LVF, RVF, or simultaneously to BVF, against a dark background. Image size was 8 cm wide and 13 cm high (sustaining a visual angle of $\sim 11.27^\circ \times \sim 18.37^\circ$ 40 cm from the screen). Stimuli were centred vertically with the innermost edge at 11 cm ($\sim 15.45^\circ$) left or right of the central fixation cross. Mean luminance of the happy faces was 6.425 cd/m^2 , of the fearful faces 6.95 cd/m^2 , and of the neutral faces 6.755 cd/m^2 . There was no significant difference in overall luminance among happy, fearful, and neutral face sets ($P > 0.4$ for all comparisons in Mann–Whitney U tests). Mean luminance of the dark background was 0.02 cd/m^2 .

The apparatus was the same as in Experiment 1.

Procedure

There were four possible conditions for each of the two emotions: an emotional face in the LVF, in the RVF, two identical copies of the same actor expressing the same emotion to BVF (bilateral congruent condition), two photographs of the same actor, one showing an emotional expression and the other, in the opposite

hemifield, showing a neutral expression (bilateral incongruent condition).

A go/no-go task was used requiring subjects to press the response key when a face (regardless of its position or number) conveyed the pre-specified target expression and to withhold from reacting when seeing the other (non-target) expression. The target expression (happy or fearful) was fixed for each block of trials and was verbally announced by the experimenter at the beginning of each block.

Four blocks were run and the presentation followed an ABBA or BAAB design (A = happy faces as target, B = fearful faces as target) with each sequence applied to half of the subjects. Each block comprised 256 randomized target trials (64 repetitions of 'go' trials for each stimulus condition; i.e. target emotion in the LVF, RVF, BVF Congruent, and BVF Incongruent) and 128 catch trials (32 repetitions of 'no-go' trials for each condition; i.e. non-target emotion in the LVF, RVF, BVF Congruent, BVF Incongruent). Overall, there were 128 repetitions of target and 64 repetitions of non-target trials for each stimulus condition and emotion. Before testing took place, the subjects underwent a practice block of 40 target and 24 non-target trials.

The pointing procedure and the balancing of response hand were identical to those used in Experiment 1.

Results

Latency and accuracy analysis

The RTs for correct responses were analysed by a $2 \times 2 \times 4$ ANOVA with three within-subjects factors: response hand (left vs. right), facial expression (happy vs. fearful), and stimulus condition (unilateral LVF, unilateral RVF, bilateral congruent, bilateral incongruent). Mean RTs are reported separately for each hand in Fig. 5 as a function of facial expressions and stimulus conditions.

The main effect of response hand was statistically significant, with faster RTs with the right hand [$F(1,24) = 5.23$, $P = 0.03$]. The effect of facial expression was also significant, indicating faster RTs for happy than for fearful faces [$F(1,24) = 21.39$, $P = 0.0001$], as was the factor stimulus condition [$F(3,72) = 14.55$, $P < 0.0001$]. No interaction was significant. Post hoc comparisons among the four stimulus types revealed a significant difference between the unilateral left and right conditions, with faster responses for LVF stimuli ($P = 0.014$). The difference between the bilateral congruent condition and the fastest (left) unilateral condition was also significant ($P = 0.036$), whereas the difference between the unilateral LVF and the bilateral incongruent condition did not reach statistical significance ($P = 0.54$). Since the effect of response hand did not interact with any other factor, thus ruling out any interpretation in terms of stimulus-response compatibility effect, we did not further analyse this factor as it lays outside the aims of the present study.

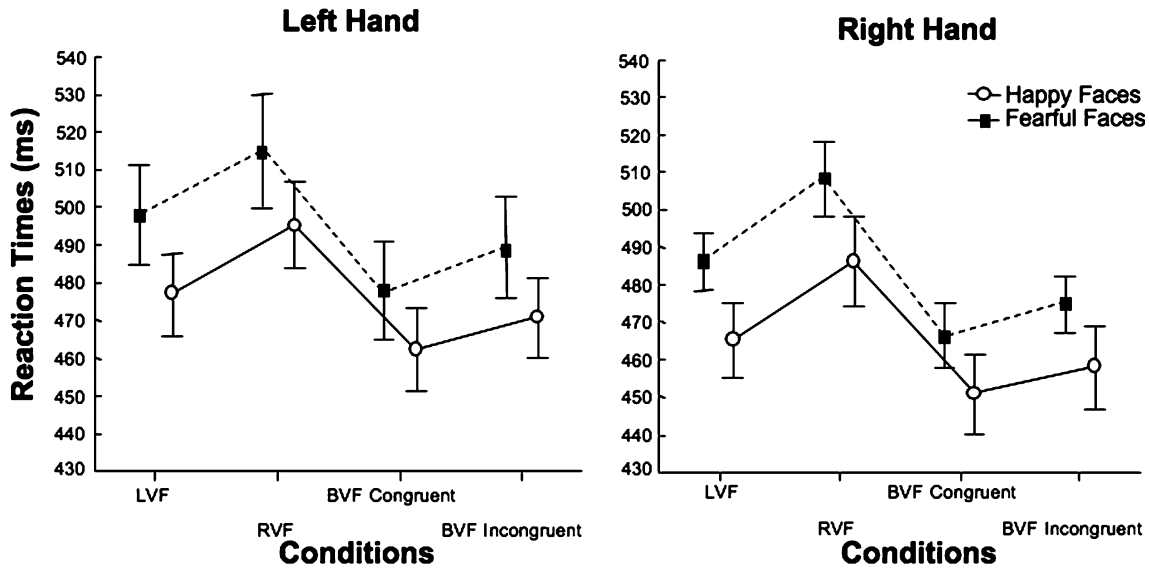


Fig. 5 Mean RT and SE for left and right response hand as a function of the four stimulus conditions and the two emotions

RTs in the BVF congruent condition were significantly faster than those in the LVF condition, for both happy and fearful faces, almost throughout the entire distribution of RTs [for happy faces from the 1st to the 98th percentile: $t(24) \geq 1.97$, $P \leq 0.029$; for fearful faces from the 1st to the 83rd percentile: $t(24) \geq 1.78$, $P \leq 0.043$], as well as the briefer latency for unilateral left faces as compared to the unilateral right [for happy faces from the 3rd to the 99th percentile: $t(24) \geq 1.87$, $P \leq 0.038$; for fearful faces from the 2nd to the 93rd percentile: $t(24) \geq 1.73$, $P < 0.048$] (Figs. 6, 7).

Errors were analysed separately for misses and false positives. Percentages of misses for LVF, RVF, BVF congruent, and BVF incongruent conditions were, respectively, 2.44, 2.34, 2.94, and 6.03% for happy faces, and 2.19, 2.03, 1.88, and 5.03% for fearful faces. An ANOVA with the same factors and levels considered in the latency analysis revealed only a main effect of stimulus condition [$F(3,72) = 8.36$, $P = 0.0001$]. Post hoc testing showed a significant difference of the BVF incongruent condition with respect to all three remaining conditions ($P < 0.0034$ for all comparisons), reflecting somewhat lower accuracy for the incongruent than for the other conditions.

Percentages of false positives for LVF, RVF, BVF congruent, and BVF incongruent conditions were, respectively, 11.38, 12.63, 11.06, and 11.94% for happy faces, and 12.44, 12.81, 11.94, and 14.5% for fearful faces. The ANOVA showed no significant main effect or interaction.

Evidence for interhemispheric cooperation

Figure 8 reports the differences between the race inequality limit (i.e. sum of the two unilateral conditions) and the two CDFs for the BVF congruent and

incongruent condition with happy faces. Figure 9 presents the same differences for fearful faces.

The pattern of violation of the race inequality was statistically significant for both emotions only with bilateral congruent faces and not with bilateral incongruent expressions (for happy faces from the 1st to the 12th percentile: $t(24) \geq 2.02$, $P \leq 0.025$; for fearful faces from the 1st to the 19th percentile: $t(24) \geq 1.88$, $P \leq 0.037$).

Discussion

The findings reported thus far provide clues concerning our main queries; that is, (a) how the perception of emotions from faces is lateralized in the brain, (b) the nature of this functional asymmetry, and (c) whether the cerebral hemispheres interact in emotional processing from faces.

As far as the first issue is concerned, the faster responses observed here for unilateral LVF than RVF emotions, regardless of valence, clearly support a model assuming that the perception of emotions is lateralized in the RH. Accordingly, the right-hemisphere hypothesis argues that this hemisphere is more strongly involved in emotional processing, whatever the valence (Borod et al. 1998). In contrast, the valence hypothesis predicts faster RTs when happy faces are projected in the RVF, thereby involving the LH, and faster RTs for fearful faces presented in the LVF/RH, which was clearly not the case. Since the hand participants used for providing responses did not interact with any other factor, this difference between unilateral conditions cannot be attributed to confounding factors such as stimulus-response compatibility effect. Rather, it more likely reflects a true superiority of the RH in emotional processing. For these reasons, in the next experiment, while continuing alter-

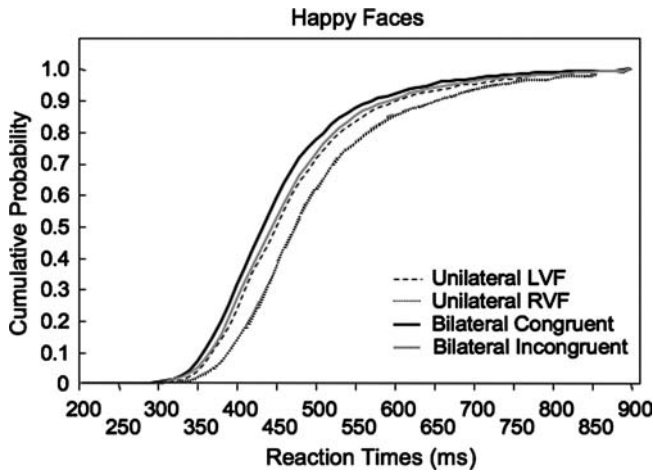


Fig. 6 CDFs of the mean RTs for happy faces as a function of the four stimulus conditions. Note the ample segregation between unilateral LVF and RVF distributions and between CDFs for LVF and BVF congruent condition

nating response hand over blocks, we did not further analyse the response-hand factor.

The bilateral gain shown with the simultaneous presentation of two congruent emotional faces, either happy or fearful, suggests that the nature of this functional specialization is relative rather than absolute. The mere presence of two faces as such cannot account for this effect, as two simultaneous faces were also presented in the incongruent condition where no RTE was observed. Our findings are also unlikely to result from congruency in the personal identity of the actors per se. Indeed, in the bilateral incongruent condition two faces of the same person were presented, one with an emotional and the other with a neutral expression. Nonetheless, a bilateral gain occurred only when the stimuli were emotionally congruent, whereas pairs of incongruent expressions did not significantly reduce RTs compared to the best unilateral condition.

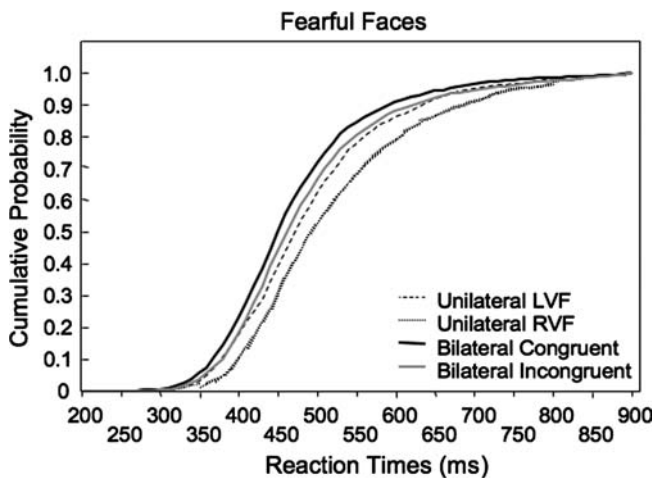


Fig. 7 CDFs of the mean RTs for fearful faces as a function of the four stimulus conditions

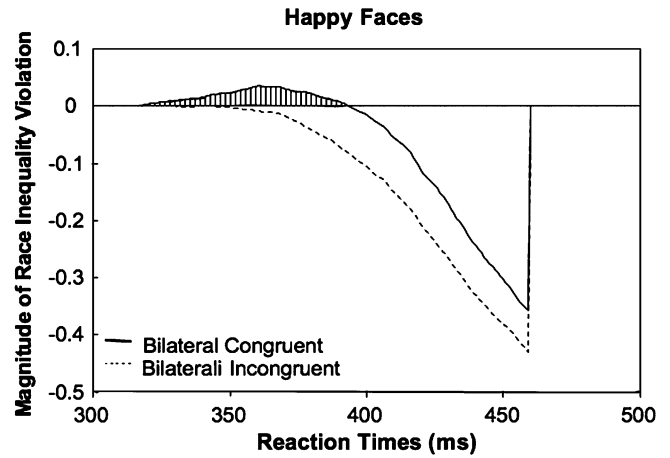


Fig. 8 Violation of the race model for congruent happy faces. Violations are indicated by positive values and vertical hatching

The violation of the inequality test for congruent happy and fearful faces shows that the bilateral gain cannot be explained by statistical facilitation. Rather, it suggests that the cerebral hemispheres interact and cooperate in the perception of emotions from facial expressions, and that this interaction is actually responsible for the more efficient processing of emotions in the bilateral congruent condition.

A final interesting finding is the overall faster RTs to happy than to fearful facial expressions. Many prior studies have shown faster RTs to positive than negative faces. Indeed, shorter latencies have been reported for expressions of happiness as compared to expressions of sadness (Crews and Harrison 1994; Feysereisen et al. 1986; Kirita and Endo 1995; Stanners et al. 1985), anger (Billings et al. 1993; Harrison et al. 1990; Hugdahl et al. 1993; Leppänen et al. 2003), disgust (Ducci 1981; Leppänen et al. 2003; Stalans and Wedding 1985), and emotional neutrality (Hugdahl et al. 1993). This is, however, the first time that the RTs benefit for happy

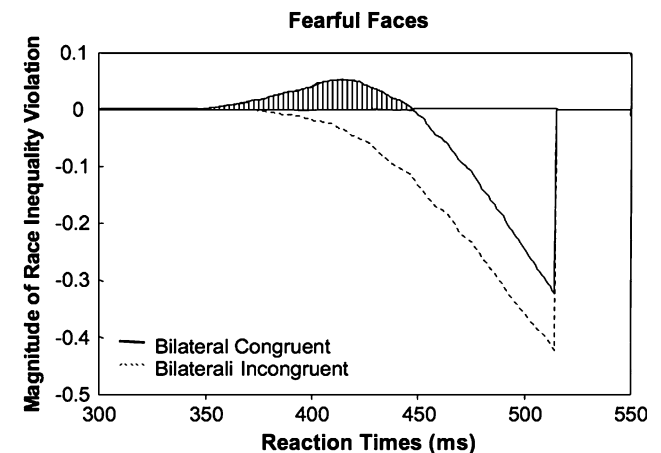


Fig. 9 Violation of the race model for congruent fearful faces. Violations are indicated by positive values and vertical hatching

faces is obtained in comparison to fearful faces. Despite its consistency, the explanation for the RTs advantage for happy faces is still the subject of debate. A possible interpretation for this finding may relate to differences in the visual features of positive and negative facial expressions. For instance, happy expressions contain fewer overlapping features with other emotional expressions than discrete negative expressions do (Johnston et al. 2001). In fact, negative expressions share many perceptual features that may account for mutual confusions between two negative expressions. Happiness, on the other hand, may be conveyed by a single salient facial feature (a smiling mouth), thus lacking the complete visual analysis of the stimulus otherwise required for negative expressions (Adolphs 2002; Fabre-Thorpe et al. 2001). Another possibility is that negative emotions are, in general, processed in a more complex and less conclusive way than positive emotions (Baumeister et al. 2001).

The present findings support and extend to normal observers and to positive emotions previous results on interhemispheric summation for emotional faces in a blindsight patient (de Gelder et al. 2001, Experiment 3) and are also consistent with a recent study showing enhanced interhemispheric communication for facial expressions (Compton et al. 2005). Conversely, our data contrasts with that reported by Schweinberger et al. (2003, Experiment 2), who also studied the effects of unilateral and bilateral presentation of affective facial expressions in a similar group of healthy volunteers. In their study, unlike ours, they failed to see any hemispheric functional asymmetry and bilateral gain. Despite the apparent inconsistencies, our and Schweinberger et al.'s studies differ in many methodological respects, thus precluding any simple or direct comparison. The most likely explanation for their negative results regards the different task demand. Here we used, like in de Gelder et al.'s study (2001), a go/no-go procedure, whereas Schweinberger et al. (2003) adopted a choice reaction time procedure. According to Grice and Canham (1990) and Grice and Reed (1992), the go/no-go procedure is likely to be more sensitive in demonstrating a redundancy gain than the choice RT. Indeed, Grice and Canham (1990) and Grice and Reed (1992) replicated, using the go/no-go procedure, two letter identification experiments previously conducted with a choice RT task. In both studies, when using the go/no-go task a redundancy gain was obtained in the two-target condition as compared to a single target presented alone, whereas in the choice RT experiments no such effect was reported. Therefore, the extant results with emotional faces parallel previous findings with verbal material, and cast doubts on the appropriateness of the choice RT method when investigating functional asymmetries and interhemispheric cooperation.

Another discrepancy concerns data analysis. Whereas Schweinberger et al. (2003) submitted mean RTs only to analyses of variance, we also plotted the entire CDFs for

all the conditions of presentation. As mentioned before, analyses based only on mean values may lead to inconsistent findings (Ratcliff 1979). This is even more remarkable considering that the authors scored responses within 200–1,800 ms as correct, although latencies slower than 1,000 ms (or 2SD) are generally regarded as delays and discarded from analyses (e.g. de Gelder et al. 2001; Hasbrooke and Chiarello 1998; Kovisto 2000; Marzi et al. 1996; Miniussi et al. 1998; Mordkoff and Miller 1993). Furthermore, even though stimulus eccentricity was only 2.9°, Schweinberger and colleagues did not provide any control for eye movements. So, it was not possible for the authors to ensure that the two halves of the screen fell into the corresponding halves of the subject's visual field when the stimuli were presented. In our study, in contrast, the pointing procedure ensured a strict control of eye movements, the stimuli were sufficiently eccentric to project to one hemisphere alone, and the exposure time (200 ms) was too brief to allow saccades during presentation. Lastly, we used a limited set of standardized stimuli (12), whereas Schweinberger et al. (2003) presented 32 different pictures of emotional faces that had not been previously validated.

Before concluding that emotional congruency between the two faces presented in the opposite hemifields was the determinant of the bilateral gain observed here, we should first rule out possible alternative explanations for our data. Indeed, the BVF congruent and incongruent conditions differed in another respect apart from emotional congruency. Whereas in the former condition there was both a physical and an emotional identity between stimuli (i.e. the faces projected were two identical copies of the same picture), the emotionally incongruent faces in the latter condition were also physically different. Thus, it is possible that the bilateral gain obtained with the congruent faces was not because they had the same emotional expression but because they were physically identical. Given this unbalanced situation, we cannot reach a definite conclusion on the nature of redundancy itself from the results of Experiment 2, since the relative contribution of emotional and physical identity cannot be disentangled. This leads to the issue of the conditions under which redundancy occurs. In other words, is redundancy for emotional faces dependent on the physical identity of the stimuli? To what extent are physically different faces redundant, if they share the same emotional meaning?

The next experiment represents an attempt to investigate these topics. We therefore replicated Experiment 2 with the inclusion of a second bilateral congruent condition in which there was only emotional but not physical identity between stimuli. Hence, in this condition two pictures of physically different faces conveying the same emotion were presented. By comparing the two BVF emotional congruent conditions (with and without physical identity) it is possible to draw inferences of the relative contribution of emo-

tional and perceptual congruency on bilateral gain and interhemispheric cooperation for affective facial expressions.

Experiment 3

Method

Participants

Twenty subjects (15 women) who did not participate either in [Experiment 1](#) or [2](#) were tested in this third experiment ($M = 24.55$ years, $SD = 3.8$, age range = 22–28). Most of the volunteers were right handed ($M = 67.02$, $SD = 24.8$) (Oldfield 1971).

Stimuli and apparatus

The stimuli were identical to those used in [Experiment 2](#), except that only photographs with happy and fearful facial expressions were used here.

We used the same apparatus adopted in the previous experiments.

Procedure

The first three conditions of stimulus presentation were identical to those of [Experiment 2](#). So, in the unilateral trials a single emotional face was presented either to the LVF or to the RVF. In the bilateral trials two identical copies of the same actor expressing the same emotion were projected. Thus, in this third condition there was both a physical and emotional identity between stimuli (BVF congruent identity). In addition, a fourth condition was set (BVF congruent emotion). Here the two copies of stimuli were congruent only at the level of emotional meaning, since two different faces of diverse actors (always one male and one female) expressing the same emotion were flashed.

Overall, there were 128 presentations of target trials and 64 repetitions of non-target trials for each type of stimulus condition and emotion (LVF, RVF, BVF congruent identity, and BVF congruent emotion).

In all other respects the procedure was identical to that adopted in [Experiment 2](#).

Results

Latency and accuracy analysis

We carried out a 2×4 repeated-measures ANOVA on mean RTs for correct responses with the factors of facial expression (happy vs. fearful) and stimulus condition (unilateral LVF, unilateral RVF, BVF congruent iden-

tity, BVF congruent emotion). Mean RTs for the four conditions and the two emotions are shown in [Fig. 10](#).

The main effect of facial expression was statistically significant [$F(1,19) = 19.72$, $P = 0.0003$], as well as the main effect of stimulus condition [$F(3,57) = 21.9$, $P < 0.0001$]. There was no significant interaction between these two factors. Post hoc tests showed that the RTs for LVF presentations significantly differed from both RVF and BVF congruent identity conditions ($P = 0.037$ and $P = 0.002$, respectively). Hence, the results reported in [Experiment 2](#) have been successfully replicated. In addition, the difference between the best unilateral (LVF) and the BVF congruent emotion condition was also significant ($P = 0.0086$), revealing that the bilateral gain was present even when the stimuli were emotionally congruent but physically different. The difference between the two BVF congruent conditions was not significant ($P = 0.97$).

The analysis of the CDFs confirmed the results obtained in the ANOVA, as the bilateral advantage was observed for both happy and fearful faces, and for both BVF congruent identity and emotion conditions which, in turn, closely overlapped throughout the whole CDFs ([Figs. 11, 12](#)). Indeed, for happy faces the RTs in the LVF condition differed significantly from those in the BVF congruent identity condition from the 2nd to the 87th percentile [$t(19) \geq 1.75$, $P \leq 0.048$], and from the 2nd to the 98th percentile as compared to the BVF congruent emotion condition [$t(19) \geq 1.76$, $P \leq 0.048$]. As far as fearful faces are concerned, the LVF condition was significantly different from the BVF congruent identity and emotion conditions at all points of the CDFs [$t(19) \geq 2.59$, $P \leq 0.009$; and $t(19) \geq 2.78$, $P \leq 0.006$, respectively]. Similarly, the difference between the LVF and RVF distributions of RTs was significant for both happy and fearful faces [for happy faces from the 2nd to the 95th percentile: $t(19) \geq 1.71$, $P \leq 0.05$; for fearful faces from the 3rd to the 92nd percentile: $t(19) \geq 1.71$, $P \leq 0.05$]. Lastly, the RTs for the BVF congruent identity and emotion conditions did not significantly differ at any point of the distributions, either with happy or fearful faces.

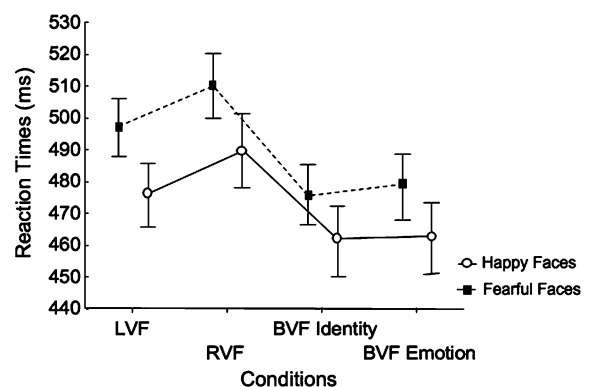


Fig. 10 Mean RT and SE as a function of the four stimulus conditions and the two emotions

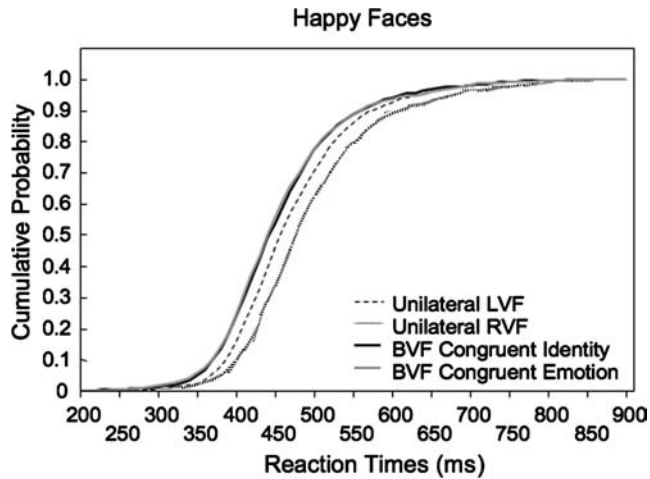


Fig. 11 CDFs of the mean RTs for happy faces as a function of the four stimulus conditions. Note the overlapping between distributions for BVF congruent emotion and identity conditions

When reacting to happy faces participants missed 3.16% of the responses to targets presented in the LVF, 3.48% in the RVF, 3.52% in the BVF Congruent Identity, and 3.2% in the BVF congruent emotion condition. The percentages of misses for LVF, RVF, BVF congruent identity, and BVF congruent emotion conditions with fearful face targets were, respectively, 3.4, 3.63, 3.01, and 3.32%. The ANOVA showed no significant main effect or interaction, suggesting that the pattern of results observed in the latency analysis cannot be attributed to speed/accuracy trade-off.

Errors in no-go trials with non-target happy faces occurred for 12.42% of the repetitions in the LVF, 16.48% in the RVF, 11.64% in the BVF congruent identity, and 8.36% in the BVF congruent emotion condition. False positives to non-target fearful faces for LVF, RVF, BVF congruent identity, and BVF congruent emotion conditions were, in that order, 12.5, 15.55, 12.42, and 7.73%. The ANOVA revealed only a significant main effect of stimulus condition [$F(3,57) = 16.12$, $P < 0.0001$]. Post hoc comparisons yielded a significant difference of the BVF congruent emotion condition by reference to all the other three conditions ($P < 0.012$ for all comparisons), thereby providing evidence for better performance with non-identical redundant than with single or identical redundant faces. Emotional faces projected in the RVF resulted in increasing errors with respect to LVF and BVF congruent identity conditions ($P < 0.03$ for both comparisons), which in turn, did not differ from each other.

Evidence for interhemispheric cooperation

The use of two BVF congruent conditions allowed us to perform two tests of the race-model inequality for each emotion: one using the CDFs from trials with two identical faces, and another using the CDFs from trials with two different targets. Figure 13 shows the differ-

ences between the race inequality limit and the two CDFs for the BVF congruent identity and emotion conditions with happy face targets. Figure 14 presents the same differences for fearful faces. As can be seen, the violation of the inequality occurred similarly for both congruent conditions (i.e. irrespectively of physical/gender identity) and for both emotions.

As far as the happy faces are concerned, this violation was statistically significant from the 1st to the 18th percentile in the BVF congruent identity condition [$t(19) \geq 1.84$, $P \leq 0.042$], and from the 1st to the 15th percentile in the BVF congruent emotion condition [$t(19) \geq 1.97$, $P \leq 0.032$]. When responding to fearful faces a neural rather than probabilistic summation was likely to occur from the 1st to the 11th percentile in the BVF congruent identity condition [$t(19) \geq 1.84$, $P \leq 0.041$] and from the 1st to the 9th percentile in the congruent emotion condition [$t(19) \geq 2.11$, $P \leq 0.022$].

Discussion

Experiment 3 provides interesting findings about the nature of target redundancy and the conditions under which the bilateral gain for emotional faces is likely to occur. Our results indicate that emotional congruency between targets is the sufficient condition for the RTE to take place. Furthermore, the lack of difference in RTs between the two emotionally congruent conditions suggests that physical and gender identity do not play any additional role in determining the bilateral gain if the information relevant for the task is the facial expression. In the same vein, a neural coactivation and interhemispheric cooperation accounted for the RTE in both congruent conditions. Thus, also at the level of interhemispheric cooperation, physical/gender differences do not seem to interfere with the mechanisms responsible for the bilateral gain, suggesting that targets can interact (via interhemispheric cross talk) even when they are

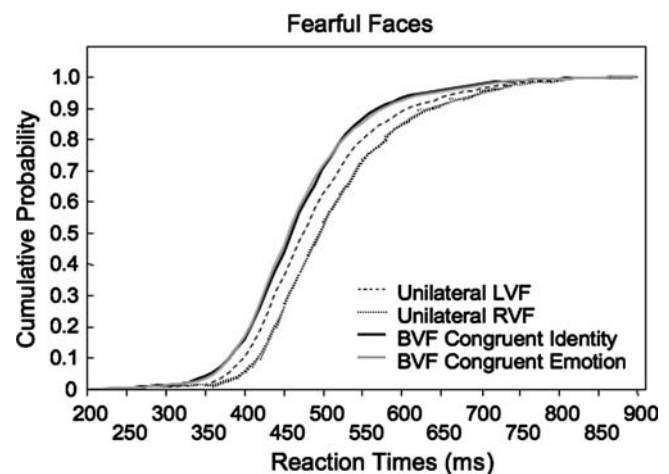


Fig. 12 CDFs of the mean RTs for fearful faces as a function of the four stimulus conditions

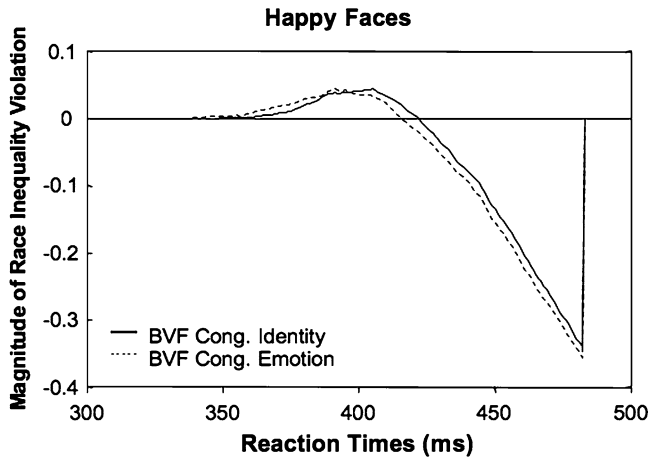


Fig. 13 Violation of the race model for BVF congruent emotion and identity happy faces. Violations are indicated by positive values

perceptually different¹. The present experiment also revealed a significantly higher accuracy (i.e. fewer false positives) with non-identical emotionally congruent faces than with identical stimuli. This finding seems to parallel a similar result reported by Grice and Reed (1990) on RTs data with upper and lowercase letters and the same paradigm adopted here. In that study, subjects had to respond to a target letter presented either in upper or in lowercase. The authors suggested that two physically different but semantically related stimuli may provide additional associative information compared

¹In principle, the RTE and the violation of the inequality test in [Experiment 3](#) might be consistent also with the interactive race model put forth by Mordkoff and Yantis (1991), and not only with neural coactivation and interhemispheric summation. Indeed, since both the BVF conditions in go trials were congruent (i.e. a BVF incongruent condition with one target and one non-target was lacking in this experiment), [Experiment 3](#) introduced contingencies among stimulus events that were absent in [Experiment 2](#) and that might have favoured the RTE and inequality violations. To test whether our participants were, in fact, sensitive to these contingencies, we performed a direct comparison of the mean RTs between identical conditions in [Experiment 2](#) (free of biased contingencies) and [3](#) (i.e. LVF, RVF, and BVF congruent identity conditions). Thus, we conducted a $2 \times 2 \times 3$ ANOVA with the between-subjects factor of experiment (Exp. 2 vs. Exp. 3) and the within-subjects factors of facial expression (happy vs. fearful) and stimulus condition (unilateral LVF, RVF, and BVF congruent identity). The results showed a significant main effect of facial expression [$F(1,43)=45.51, P<0.0001$] and stimulus condition [$F(2,86)=30.99, P<0.0001$]. Importantly, the main effect of experiment [$F(1,43)=0.035, P>0.85$] and the experiment \times facial expression [$F(1,43)=0.03, P>0.86$], experiment \times stimulus condition [$F(2,86)=0.31, P>0.73$] and experiment \times facial expression \times stimulus condition [$F(2,86)=0.06, P>0.93$] interactions were all non-significant, with the largest difference between comparable conditions in [Experiment 2](#) and [3](#) equal to 5.44 ms. This clearly indicates that the potentially useful information in favour of an enhanced bilateral gain present in [Experiment 3](#) was not actually used by our subjects who performed as in [Experiment 2](#) free of biased contingencies. Thus, even in this third experiment, the RTE and the violation of the inequality test in both the BVF conditions is likely to be the result of neural coactivation and interhemispheric summation rather than of interactive separate activation.

with a pair of stimuli that are only physically identical. This is because for two visually different stimuli a larger number of relevant features would be available for reaction. A similar explanation seems plausible also for the present results, although this effect clearly deserves further study.

Overall, our findings contrast with a position assuming that the RTE and interhemispheric coactivation are perceptual processes simply dependent on visual identity (Fournier and Eriksen 1990). Conversely, the present results indicate that, at least when meaningful stimuli are used, target redundancy is an associative rather than a mere perceptual process related to the physical identity of the targets. This is in keeping with previous studies using the RTP with various meaningful stimuli. For instance, Grice and Reed (1992) and Marks and Hellige (2003) reported a bilateral gain and an interhemispheric interaction when target letters or trigrams, one in uppercase and the other in lowercase, were presented to BVF (e.g. “A” and “a”). Similarly, Koivisto (2000) showed an RTE with two different but semantically related pictures (e.g. both animals or both objects). Finally, Ratinckx and Brysbaert (2002) demonstrated interhemispheric interaction in a number comparison task where the two numbers were of different modalities (i.e. arabic digits and word numerals). Thus, the present findings with emotional faces complement prior studies with other meaningful, but non-emotional, stimuli and indicate that interhemispheric interaction is a more complex process than simply transporting copies of information from one hemisphere to the other.

General discussion

Functional hemispheric asymmetries have been documented for many perceptual, cognitive and motor functions, revealing a degree of functional specialization

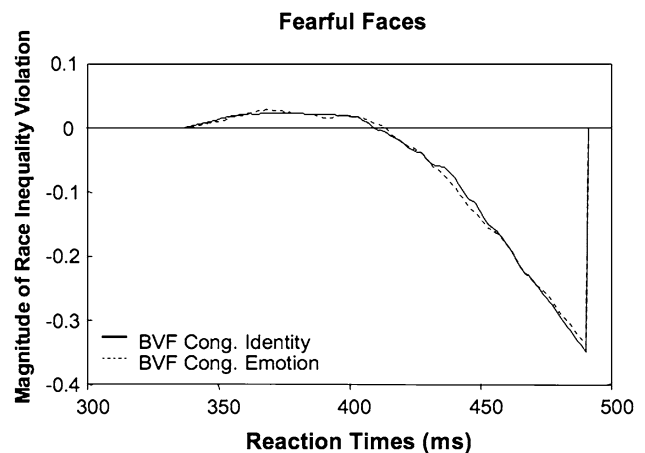


Fig. 14 Violation of the race model for BVF congruent emotion and identity fearful faces. Violations are indicated by positive values

of the hemispheres. Whether emotional processing is similarly lateralized is one of the central questions of affective neuroscience. The two most common models of emotion lateralization are the right hemisphere and the valence hypothesis (Borod et al. 1998; Canli 1999). Whereas the first hypothesis postulates that emotional processing is lateralized toward the RH, the second states that the RH is preferentially engaged with negative emotions and the LH with positive emotions. To some extent, however, the difference between these two theories depends on the meaning of the term 'emotion' since there are substantial differences in the task demands and the cognitive processes required to perform them in the available studies. According to many authors (Adolphs 2002; Oatley and Johnson-Laird 1987; Panksepp 1998; Plutchik 1980), the emotional system is organized in different, but interacting, neuro-cognitive components. For instance, the communicative aspects of emotions, the autonomic-vegetative response, or the experience of these emotions are likely to engage different neural substrates that may be lateralized in different ways across the hemispheres. The communicative processes, in turn, should be further divided into perceptual and expressive components, and into various communicative channels such as lexical, prosodic, or facial expression (Borod 1993; Borod et al. 1998). Taking all these aspects into account, a trend can be observed in the literature: the perception of emotions from facial expressions appears to be consistently lateralized, regardless of valence, toward the RH (Borod 1992; Bryden 1982; Sackeim et al. 1982). Conversely, the valence hypothesis seems to apply to the behavioural expression and/or experience of emotion (Canli 1999; Davidson 1995). This direct link between the perception of emotions from facial expressions and the RH is in keeping with the faster responses to positive and negative emotions in the LVF/RH than in the RVF/LH observed in the present study. This is also consistent with the majority of the studies investigating the perception of facial emotions in normal subjects (Bryden 1982; Bryden and Ley 1983; Christman and Hackworth 1993; Davidson 1993; Lane et al. 1995), unilateral brain-damaged patients (Adolphs et al. 2000; Blonder et al. 1991; Borod 1992; Borod et al. 1986, 1998; Bowers et al. 1985; DeKosky et al. 1980), and non-humans (Morris and Hopkins 1993; Vallortigara and Rogers 2005). Similar conclusions can be drawn from studies using event-related brain potentials (de Haan et al. 1998) and electrical stimulation techniques in humans (Fried et al. 1982), whereas findings from functional imaging contributed little to the question of functional asymmetry, mainly because hemispheric contrasts have not usually been computed (Adolphs 2002). However, also one recent fMRI study that directly addressed this issue provided evidence for right-lateralized emotional processing involving the right amygdala and the right extrastriate cortex (Noesselt et al. 2005).

The specialization of the RH for perceiving facial expressions does not mean that the LH is silent with

respect to this process. Indeed, the bilateral gain observed here clearly indicates that the LH contributes to emotional processing and, consequently, that the RH superiority is relative rather than absolute. This gain in latencies cannot be explained by probability summation or race-models, as the inequality test was violated for both emotions in the second and third experiment. Rather, a neural summation and interhemispheric cooperation is likely to have occurred. The only crucial aspect responsible for this interhemispheric interaction seems to be emotional congruency between stimuli. Indeed, physical identity between stimuli or the personal and gender identity of the faces were neither sufficient (Experiment 2) nor necessary (Experiment 3) for obtaining the RTE in the bilateral conditions. Hence, the present findings indicate that interhemispheric cooperation in the perception of facial emotions is a complex process relatively insensitive to physical identity between stimuli. Instead, it requires congruency at the level of the affective meaning gleaned from the faces.

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