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Fast recognition of social emotions takes the whole brain: Interhemispheric cooperation in the absence of cerebral asymmetry

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Abstract

Hemispheric asymmetry in emotional perception has been traditionally studied for basic emotions and very little is known about laterality for more complex social emotions. Here, we used the "redundant target paradigm" to investigate interhemispheric asymmetry and cooperation for two social emotions in healthy subjects. Facial expressions of flirtatiousness or arrogance were briefly presented either unilaterally in the left (LVF) or right visual field (RVF), or simultaneously to both visual fields (BVF) while participants responded to the target expression (flirtatious or arrogant, counterbalanced between blocks). In bilateral conditions the faces could show the same emotion (congruent condition) or two different expressions (incongruent condition). No difference between unilateral presentations was found, suggesting that the perception of social emotions is not hemispherically lateralized. Responses were faster and more accurate in bilateral displays with two emotionally congruent but physically different faces (i.e., a male and a female expressing the same emotion) than in unilateral conditions. This "redundant target effect" was consistent with a neural summation model, thereby showing that interhemispheric cooperation may occur for social emotions despite major perceptual differences between faces posing the same expression.

Keywords: Social cognition; Face perception; Hemispheric laterality; Redundant target effect; Bilateral gain; Flirtatiousness; Arrogance

1. Introduction

Human behaviors occur to a great extent in social situations and the ability to infer what other persons are feeling from watching their facial expressions is one of the most important skills in communication and social interaction. A central issue in neuropsychology and affective neuroscience concerns whether and how processing of emotional facial expressions is functionally lateralized across the hemispheres (Borod, 2000; Canli, 1999; Demaree, Everhart, Youngstrom, & Harrison, 2005). Indeed, hemispheric asymmetries reveal division of processes and provide information about the organizing principles of the brain (Hugdahl & Davidson, 2004). Furthermore, interest in functional asymmetry has led in recent years to the related question of interhemispheric interaction; that is, how, to what extent, and under which conditions the cerebral hemispheres cooperate and coordinate their respective processing abilities in order to operate more efficiently (Compton, Feigenson, & Widick, 2005; Hoptman & Davidson, 1994).

Traditional neuropsychological accounts for the neural basis of emotions have contrasted the "right-hemisphere hypothesis" to the "valence hypothesis". The former postulates a generalized right-hemisphere (RH) specialization for emotional processing regardless of valence (i.e., either for positive or negative emotions), whereas the latter assumes a preferential engagement of the RH for negative emotions and of the left hemisphere (LH) for positive emotions (Borod, 2000; Canli, 1999; Demaree et al., 2005, for reviews). This apparent inconsistency in the literature has been reconciled by recent findings indicating that the perceptual processing of both positive and negative emotions is a RH function (Borod et al., 1998; Bowers, Bauer,

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Coslett, & Heilman, 1985; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001; Noesselt, Driver, Heinze, & Dolan, 2005; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004), whereas a differential hemispheric specialization exists for displaying facial expressions and for experiencing emotions as a function of valence (Cahill et al., 1996; Davidson, 1995; Davidson, Marshall, Tomarken, & Henriques, 2000; Gray, Braver, & Raichle, 2002; Waldstein et al., 2000).

To date, however, most investigations on hemispheric specialization in the visual perception of emotions have predominantly concentrated on facial expressions of the so-called basic emotions, and virtually all that is known about functional laterality for emotions is based on such data. Basic emotions such as happiness, surprise, fear, anger, disgust, and sadness, are thought to be at least partly hardwired and signalled by specific facial expressions widely recognized across different cultures (Ekman, 1999). According to an evolutionary perspective, these basic emotions developed because of their adaptive value in dealing with fundamental life needs, providing us with fast and automatic reactions to recurrent situations relevant to survival (Darwin, 1998; Tomkins, 1962–1963; Tooby & Cosmides, 1990). Yet facial expressions encompass also more complex social signals reflecting emotional states like arrogance, flirtatiousness, admiration, and guilt; the meanings of which are learned during early development as part of the socialization process and may not be as predetermined as for basic emotions (Adolphs, 2003; Buck, 1988). Similar to basic emotions, these "social emotions" have a clear valence, either positive (e.g., flirtatiousness or admiration) or negative (e.g., arrogance or guilt). However, social emotions are typically related to the social context and the interaction with other people for their interpretation (Adolphs, Baron-Cohen, & Tranel, 2002; Baron-Cohen, Wheelwright, & Jolliffe, 1997; Shaw et al., 2005). Moreover, they are much less likely to be associated with reflex-like adaptive actions than basic emotions are.

Evidence for hemispheric asymmetry in the perception of social emotions is scant and indirect, as the few studies available in the literature focused more on processes associated with displaying facial or verbal expressions of emotions rather than on perception or recognition of these expressions in others (Buck, 1984; Buck, Losow, Murphy, & Costanzo, 1992; Gainotti, 2001; Leventhal, 1982; Ross, Homan, & Buck, 1994; Tucker, 1981). One of these studies required subjects to recall emotional life events before and after injection of amobarbital into the right and left internal carotid arteries (Wada test) for neurosurgical purposes (Ross et al., 1994). During inactivation of the RH following right-side injection, most of the patients altered their affective recall denying basic emotions and substituting with social emotions. The authors interpreted these findings as suggesting that basic emotions are modulated by the RH and social emotions by the LH. Other authors have also held a similar position on a more theoretical ground, to the extent that the RH has been associated with automatic processing and activation on innate emotional schemata and the LH with control (i.e., facilitation or inhibition) of these processes according to social rules and propositional representations (Buck, 1984; Buck et al., 1992; Gainotti, 2001; Leventhal, 1982; Tucker, 1981).

One possibility of testing hemispheric asymmetries and interhemispheric cooperation in visuo-perceptive tasks is to present stimuli tachistoscopically either unilaterally to the left (LVF) or to the right visual hemifield (RVF), or simultaneously to both hemifields (BVF), requiring subjects to perform a detection or a more demanding decision task ("redundant target paradigm", RTP) (Banich, 2004; Corballis, 2002; Dimond & Beaumont, 1972). The anatomy of the primary visual pathways is such that LVF and RVF stimuli project to the RH and LH, respectively. Thus, in unilateral conditions only one hemisphere is initially stimulated (before interhemispheric cross-talk via the corpus callosum), whereas in the bilateral condition both hemispheres are simultaneously stimulated. By comparing performance differences (in terms of latency and/or accuracy) between the two unilateral conditions, it is possible to address functional hemispheric asymmetries. In addition, a measure of interhemispheric cooperation can be obtained by contrasting the performance in the *best* unilateral condition with the performance in the condition of bilateral stimulation. Reaction times (RTs) to two simultaneous stimuli are typically faster than to a single stimulus, a phenomenon known as bilateral gain or "redundant target effect" (RTE) (Zaidel & Rayman, 1994). Given appropriate analysis it is possible to tell whether the RTE reflects genuine interhemispheric cooperation and neural summation or is instead due to probabilistic facilitation related to the presence of two targets (see Section 2 for details).

We recently used the RTP on healthy subjects to investigate functional asymmetry and interhemispheric cooperation in the perception of basic emotions (happiness and fear) (Tamietto, Latini Corazzini, de Gelder, & Geminiani, 2006; experiments 2 and 3). Our findings were three-fold: (1) we observed faster RTs to unilateral LVF than RVF emotions, regardless of valence, indicating that the perception of basic emotions is lateralized toward the RH; (2) simultaneous presentation of two congruent emotional faces, either happy or fearful, yielded an RTE consistent with interhemispheric cooperation and neural summation; (3) this interhemispheric cooperation was still present when the two faces were emotionally congruent but physically different (i.e., two different faces: one male and one female, posing the same expression), therefore pointing to emotional congruency as the most relevant aspect for interhemispheric interaction.

The aim of the present study is to extend to social emotions our initial findings on basic emotions using a similar RTP design.

2. Method

2.1. Participants

Twenty-eight healthy volunteers (18 women) contributed data for this experiment ($M = 24.64$ years, S.D. = 3.09, age-range = 20–33 years). They all reported normal or corrected-to-normal visual acuity and no history of neurological or psychiatric illness. Most of the volunteers were right-handed as assessed by the Edinburgh Handedness Inventory ($M = 78.55$ years, S.D. = 19.56) (Oldfield, 1971). The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and all participants provided written informed consent approved by the Ethical Committee of the Department of Psychology, University of Torino, Italy.

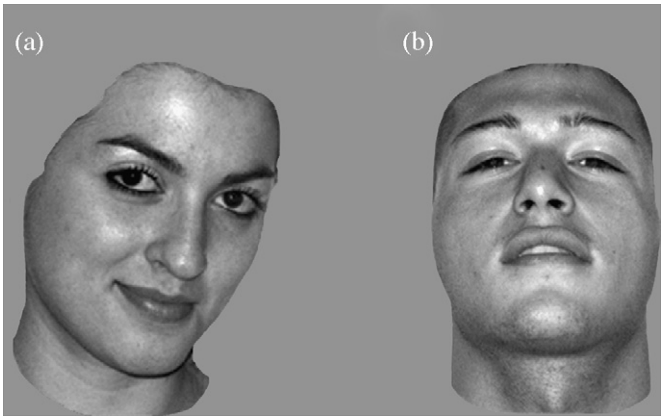

Fig. 1. Examples of the social emotion expressions: (a) flirtatiousness and (b) arrogance.

2.2. Stimulus preparation and apparatus

Ten semi-professional actors (five women) were invited to pose facial expressions of four social emotions previously studied in the literature: arrogance, admiration, flirtatiousness, and guilt (Adolphs et al., 2002; Baron-Cohen et al., 1997; Ruby & Decety, 2004; Shaw et al., 2005; Takahashi et al., 2004). In addition, the actors also showed a neutral non-expressive face. Their face was photographed with a digital camera (Nikon® Coolpix 3100) under controlled and standardized lighting conditions. The resulting 50 photographs (40 social emotions – 10 per each emotion – and 10 neutral faces) were then computer-edited (Adobe PhotoShop®) to match the following parameters: the color pictures were transformed into greyscale images and enclosed in rectangular frames 8 cm wide and 13 cm high (sustaining a visual angle of ~7.38° × ~12.25°, 60 cm from the screen); the irrelevant aspects, like hair and non-facial contours, were removed and masked in grey; and the mean luminance was set to 6.7 cd/m^2.

Stimulus selection for the present experiment was based on the results of a study with 30 persons (who did not participate in the main experiment) in which the social emotion expressions were validated ($M = 25.36$ years, S.D. = 4.14, age-range = 21–36 years). For this purpose, the stimuli were presented one by one on a touch-screen and shown for 2000 ms with 3000 ms interval, with the five labels corresponding to the five possible expressions shown in Italian below the pictures (equivalent in English to: arrogance, admiration, flirtatiousness, guilt, and neutral). The order of the five labels, from left to right, was randomized between trials. Subjects were instructed to categorize each stimulus in a forced-choice procedure as quickly and accurately as possible by touching one of the five labels on the touch-screen. The correct average recognition rate for all 10 arrogance stimuli was 89% (ranging from 80 to 100%; $p \leq 0.001$ by Binomial tests for each stimulus), for admiration it was 85% (from 80 to 100%; $p \leq 0.001$), for flirtatiousness 90% (from 80 to 100%; $p \leq 0.001$), for guilt 84% (from 80 to 100%; $p \leq 0.001$), and for neutral expressions 99% (from 93 to 100%; $p \leq 0.0001$). Overall there was a significant consistency between intended (i.e., posed) and judged expressions (Cohen $K = 0.87$, $p \leq 0.0001$).

Flirtatiousness and arrogance were chosen as the two emotions for the actual experiment. Out of the remaining 30 stimuli (10 for flirtatiousness, 10 for arrogance, and 10 neutral) the 12 highest-ranked pictures were selected, all of which were recognized with 100% accuracy (4 actors, 2 males and 2 females each with either a flirtatious, arrogant, or neutral expression) (Fig. 1).

These 12 photographs were presented for 200 ms in the LVF, RVF, or simultaneously to BVF, against a dark background on a 21 in. CRT monitor. Stimuli were centred vertically with the innermost edge at 11 cm (~10.3°) left or right of the central fixation cross. Mean luminance of the dark background was 0.2 cd/m^2.

The monitor was connected to an IBM-compatible Pentium PC controlling stimulus presentation and response recording by means of Presentation 9.3 software (Neurobehavioral Systems®). Participants responded by key pressing on a response box (RB-610, Cedrus Corporation®). Eye movements were monitored via an infrared camera (RED-III pan tilt) connected to an eye-tracking system that analyzed on-line monocular pupil and corneal reflection (sampling rate 50 Hz) (iViewX, SensoMotoric Instruments®).

2.3. Procedure

Participants were tested in a dimly-lit room during an experimental session lasting approximately 1.30 h. They were seated at a distance of ~60 cm from the monitor, the vertical midline of which lay on the sagittal midplane of their trunk and head. Each trial started with a central fixation cross (1.5 cm × 1.5 cm; ~1.26° × 1.26°) that remained on the screen until proper fixation (here defined as the persistence of the eye gaze on the screen for at least 500 ms within the cross area; 2.25 cm^2). At fixation the stimuli were immediately flashed for 200 ms, thereby avoiding the need to replace trials previously discarded because of unsteady fixations. A blank screen lasting 2800 ms followed stimulus presentation and lasted until next trial start.

There were four equiprobable conditions for each of the two social emotions: (1) an emotional face in the LVF; (2) same in the RVF; (3) two faces of different actors (always one male and one female) expressing the same emotion to BVF (congruent condition); (4) two faces (again one male and one female) one showing an emotional expression and the other, in the opposite hemifield, showing a neutral expression (incongruent condition). Therefore, this design controlled for possible confounding factors due to physical/gender differences between pairs of stimuli in the two bilateral conditions so that in both conditions the two faces differed equally in their physical/gender properties and varied only in the relevant dimension of emotional congruency.

A go/no-go task was used requiring subjects to press the response key as fast and as accurately as possible 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 (flirtatiousness or arrogance) was fixed for each block of trials and was verbally announced by the experimenter at the beginning of each block. Response hand was balanced between blocks. Half of the subjects started with the right hand, half with the left, changing hand after each block.

Four blocks were run and the presentation followed an ABBA or BAAB design (A = flirtatiousness as target, B = arrogance 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.

2.4. Data analysis

2.4.1. Assessment of hemispheric asymmetry and RTE

Response latency and accuracy were analyzed. A $2 \times 2 \times 4$ repeated-measures analysis of variance (ANOVA) was conducted on mean RTs for correct responses with three within-subjects factors: response hand (left versus right), facial expression (flirtatious versus arrogant), and stimulus condition (LVF, RVF, BVF congruent, BVF incongruent). Responses faster than 200 ms and slower than 1000 ms from stimulus onset were respectively considered as anticipations and delays, and were removed from analysis. Actually, they represented a minuscule minority (<1%).

Errors were analyzed separately for misses and false positives by two ANOVAs with the same factors and levels considered in the latency analysis. Post hoc Scheffé test was chosen to further analyze significant main effects and interactions.

2.4.2. Test of interhemispheric cooperation

Observation of RTE is not *per se* conclusive of interhemispheric cooperation. Indeed, separate-activation or race models account for a bilateral gain simply relying on the fact that the probability of a fast detection increases with the number of targets (Raab, 1962; Townsend & 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 (the fastest to be processed) is directly responsible for the response also on bilateral trials. Since speed of processing is a random variable, multiple stimuli are on average more likely to yield a faster response than single stimuli for purely probabilistic reasons. In contrast, coactivation models assume the presence of a functional interaction and interhemispheric cooperation (also called neural summation) between perceptual channels that results in a reduction of response time (Colonius, 1986, 1988; Miller, 1982, 1986; Ulrich & 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 with only one target.

To discriminate between probabilistic and neural coactivation models we used the inequality test of Miller (1982, 1986). This test is based on cumulative distribution functions (CDFs) for RTs and sets an upper limit on the facilitation produced by bilateral stimuli for any time t assuming separate-activation:

$$P(\mathrm{RT} \leq t|\mathrm{SL\ and\ SR}) \leq P(\mathrm{RT} \leq t|\mathrm{SL}) + P(\mathrm{RT} \leq t|\mathrm{SR}),$$

where $P(\mathrm{RT} \leq t|\mathrm{SL\ and\ SR})$ is the cumulative probability of a correct detection with bilateral stimuli, $P(\mathrm{RT} \leq t|\mathrm{SL})$ is the cumulative probability of a response given one target in the LVF, and $P(\mathrm{RT} \leq t|\mathrm{SR})$ is the cumulative probability of a response given one target in the RVF. Since separate-activation or race models predict no interaction between channels (hemispheres), the probability of responding to redundant stimuli by time t cannot be higher than the sum of the probabilities associated to either unilateral stimuli. Thus, the violation of the inequality test indicates a bilateral gain that exceeds the upper limit of probability summation and is consistent with an interpretation in terms of neural summation and interhemispheric cooperation; otherwise a probabilistic facilitation better explains the effect.

To obtain the CDFs, we first rank-ordered RTs in each subject and for each condition and emotion. 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 and emotion were then obtained simply by averaging across subjects all the RTs at each percentile. The significance of the inequality violation was assessed by a series of paired-sample t-tests at each percentile of the CDFs in which a violation occurred descriptively.

3. Results

3.1. Latency and accuracy analysis

Mean RTs are shown separately for each response hand in Fig. 2 by facial expressions and stimulus conditions.

There was no significant main effect of response hand or facial expression, and no significant interaction [$F(1, 27) = 0.87$, $p = 0.36$; $F(1, 27) = 0.028$, $p = 0.87$, respectively]. Only the main effect of stimulus conditions turned out to be significant, $F(3, 81) = 20.38$, $p < 0.0001$, with faster responses in the BVF congruent condition with respect to the three remaining display types, thereby showing a bilateral gain for BVF congruent expressions ($p < 0.0001$ for all post hoc comparisons on the stimulus condition factor). By contrast, the post hoc comparison between the unilateral LVF and RVF conditions was not statistically significant ($p = 0.96$), as well as the comparisons between the BVF incongruent and unilateral conditions ($p > 0.35$, for both comparisons). This similar performance for unilateral LVF and RVF displays indicates absence of significant hemispheric asymmetries in latency data.

Table 1
Mean percentage (±S.E.) of target expressions missed in "go" trials

Conditions	Target emotions	
	Flirtatiousness	Arrogance
LVF	2.59% (±0.54)	2.40% (±0.42)
RVF	2.58% (±0.50)	2.23% (±0.39)
BVF congruent	1.73% (±0.32)	2.09% (±0.34)
BVF incongruent	2.15% (±0.36)	2.27% (±0.29)

Table 2
Mean percentage (±S.E.) of false positives in "no-go" trials

Conditions	Non-target emotions	
	Flirtatiousness	Arrogance
LVF	11.64% (±1.63)	10.71% (±1.11)
RVF	11.27% (±1.42)	11.08% (±1.28)
BVF congruent	11.58% (±1.68)	10.10% (±1.14)
BVF incongruent	10.80% (±1.49)	10.07% (±1.36)

Mean percentages of misses and false positives are shown in Tables 1 and 2 by emotions and display types.

The ANOVA on misses reported only a significant main effect of stimulus conditions, $F(3, 81) = 3.6$, $p = 0.017$, with fewer errors in the BVF congruent than in the LVF condition ($p = 0.033$), but no difference between the two unilateral presentations ($p = 0.97$).

The analysis of false positives showed no significant main effect or interaction.

Therefore, accuracy findings complement the results observed in the latency analysis and indicate that the RTE for BVF congruent expressions, as well as the lack of significant

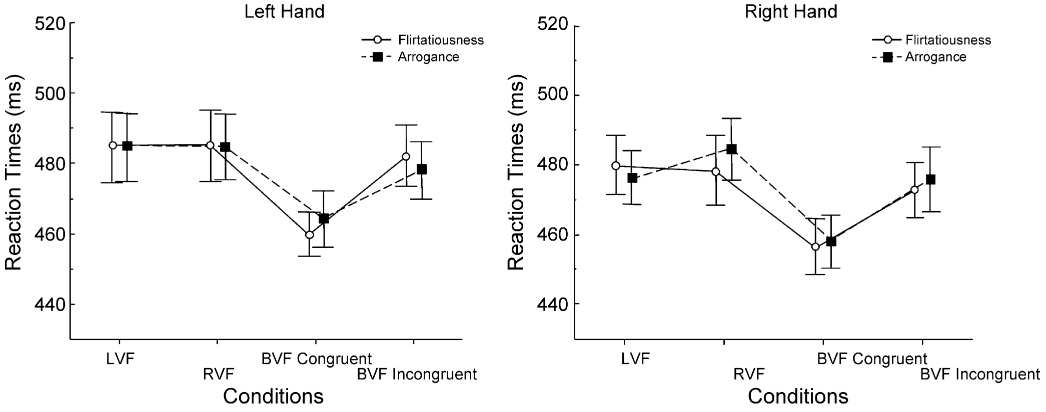

Fig. 2. Mean RTs and standard errors (S.E.s) for left and right response hand as a function of stimulus conditions and target expressions.

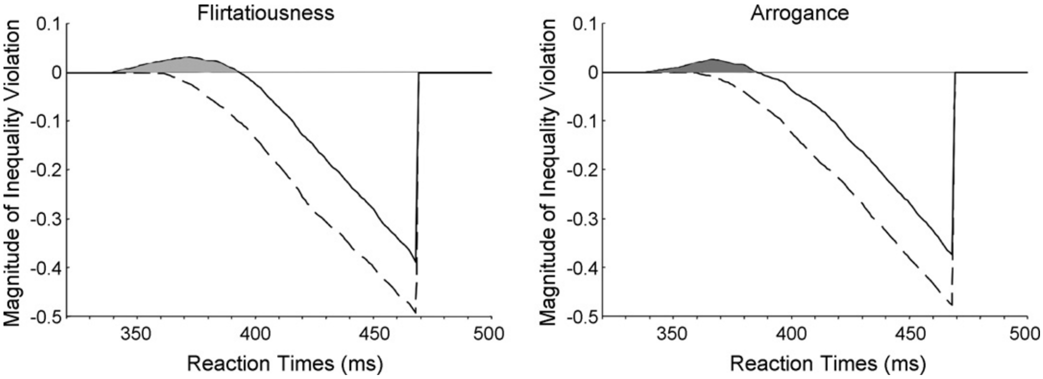

Fig. 3. Differences between the CDFs for bilateral congruent and incongruent conditions and the race inequality limit for flirtatious and arrogant target expressions separately. Violations are indicated by positive values and the grey area.

differences between unilateral conditions, cannot be attributed to speed/accuracy trade-off.

3.2. *Test of interhemispheric cooperation*

Fig. 3 reports separately for flirtatiousness and arrogance 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 conditions.

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, thereby arguing for interhemispheric cooperation (for flirtatious expressions from the 1st to the 9th percentile, $t(27) \geq 1.74$, $p \leq 0.038$; for arrogant expressions from the 1st to the 8th percentile, $t(27) \geq 1.85$, $p \leq 0.043$).

4. Discussion

Functional hemispheric asymmetry for emotions is a classic topic in neuropsychology and it has long been known that the LH and RH process different aspects of emotions, although the precise way in which they do so has been elusive. In the present study we provide new findings about interhemispheric asymmetry and cooperation in the recognition of faces expressing social emotions. Our main thrust is to have shown that social emotions are recognized by the LH and RH with comparable readiness and accuracy, and that the simultaneous involvement of both hemispheres enhances the performance and leads to interhemispheric cooperation.

The few prior studies that have investigated complex social emotions and their possible hemispheric lateralization have proposed that the LH might be associated with social emotions and the RH with basic emotions (Buck, 1984; Buck et al., 1992; Gainotti, 2001; Leventhal, 1982; Ross et al., 1994; Tucker, 1981). The lack of significant differences in RTs and accuracy between unilateral presentations of social emotions reported here cannot be accommodated by this hypothesis, and also confines the explanatory power of the “right-hemisphere hypothesis” to the recognition of basic emotions in the affective domain. As noted earlier, social emotions are defined with reference to social situations and understanding of social norms, their decoding relies in part on social knowledge and on the ability to represent the metal states of others (theory of mind, ToM) (Adolphs, 2003; Frith & Frith, 1999). To this extent, it seems likely that such a plethora of social/cognitive functions is broadly represented in the whole brain. We thus speculate that, whereas the recognition of basic emotions appears to be initially mediated by the RH, the recognition of social emotions from facial expressions is not hemispherically lateralized. To our knowledge, neuroimaging and lesion studies on the neural substrates of social cognition have seldom tackled the issue of hemispheric asymmetry for the perception of full facial expressions of social emotions. Yet, indirect evidence appears to support the non-lateralized perspective on social emotions retained here.

Neuroimaging studies have shown that the evaluative process of social emotions is mediated by a neural network including homologous regions of the two hemispheres. Bilateral activation of the middle prefrontal cortex (mPFC) has been consistently reported in a variety of tasks related to social cognition and ToM (Baron-Cohen et al., 1999; Castelli, Happe, Frith, & Frith, 2000), and is reduced in autistic patients, who are impaired in their ability to recognize complex mental states in others (Castelli, Frith, Happe, & Frith, 2002; Frith, 2001). Besides the mPFC, the ability to make inferences about others’ mental states also involves the paracingulate cortices, superior temporal sulci and temporal poles of both hemispheres (Frith & Frith, 1999; Gallagher et al., 2000; Walter et al., 2004; Winston, Strange, O’Doherty, & Dolan, 2002). Notably, the joint activation of these areas in both hemispheres has been reported when subjects were asked to recognize complex mental states, social emotions included, from images of the eye region of the face (Baron-Cohen et al., 1999).

Lesion studies complement the foregoing neuroimaging results, showing that deficits in social cognition may incur following unilateral brain damage to the LH as well as RH. Patients with unilateral lesions to the frontal lobes are comparably impaired in the attribution of mental states to others when the damage is to either the LH or RH (Rowe, Bullock, Polkey, & Morris, 2001). Likewise, recognition of social emotions from expressions around the eye region is impaired after unilateral damage to the left as well as right amygdala (Adolphs et al., 2002; Shaw et al., 2005). However, evaluation of other social characteristics on the basis of full facial appearance, like trustworthiness and approachability, is significantly impaired only after bilateral amygdala damage (Adolphs, Tranel, & Damasio, 1998).

Overall, these findings urge caution in the rigid assignment of cognitive processes to neural structures, as it is probable that a given structure participate in several processes, depending on the time at which its activity is sampled and on details of the task and context. Nevertheless, the bulk of the data seems to converge on two main points: (1) recognition of social emotions from face recruits a broad range of cognitive functions mediated by different neural structures; (2) these structures are likely distributed in homologous regions of the LH and RH, so that both hemispheres have competences, though not necessarily of the same kind, in decoding social emotions. Both these points are in line with the lack of hemispheric differences reported in the present study and are notably coherent with our conjecture about a non-lateralized perceptual processing of social emotions.

Bilateral presentation of two congruent social emotions, either of flirtatiousness or arrogance, led to shorter latency and fewer misses by reference to the unilateral conditions. As previously reported for basic emotions, even in this case an interhemispheric cooperation accounted for the RTE (Tamietto et al., 2006). This finding fits well with the foregoing lack of functional laterality and the seemingly balanced involvement of the two hemispheres in decoding social emotions. Indeed, it has been suggested that coordinating processing across hemispheres is particularly beneficial when both hemispheres have competences that may contribute to task execution and when redundant stimuli activate transcortical cell assemblies located in homologous areas within the two hemispheres (Hugdahl & Davidson, 2004; Pulvermuller & Mohr, 1996). Importantly, this neural summation occurred despite major perceptual differences between the faces and even when a fine-grained visual processing is envisaged, as with the recognition of social emotion expressions. This extends our knowledge of the mechanisms for interhemispheric cooperation in the affective domain beyond basic emotions, and suggests that emotional congruency between targets is the sufficient condition for the neural RTE to take place. Thus, our results concur with others to indicate that interhemispheric cooperation may involve rather abstract aspects of information processing like semantic or emotional meaning (Grice & Reed, 1992; Koivisto, 2000; Marks & Hellige, 2003; Ratinckx & Brysbaert, 2002; Tamietto et al., 2006).

Interestingly, the fact that interhemispheric cooperation does not seem sensitive to physical identity is consistent with our current knowledge of its possible neural underpinnings and with what is known about interhemispheric connections. Compared to “associative” areas, early sensory cortices of the two hemispheres are not extensively interconnected across the corpus callosum (Marzi, 1986). The primary visual cortices have callosal connections only for visual field representation close to the vertical meridian (Pandya & Seltzer, 1986), whereas later portions of the ventral visual stream in extrastriate areas are more heavily interconnected (Essen & Zeki, 1978). Consequently, the visual representations shared by means of the corpus callosum are predominant at later stages of analysis and apparently rely on higher visual properties not constrained by specific stimulus features. Therefore, the presence of an RTE of the neural type with stimuli presented at peripheral visual locations and despite physical differences is coherent with current neurophysiological and neuroimaging evidence pointing to extrastriate cortex and superior colliculi as the possible neural substrates mediating interhemispheric summation (Iacoboni, Ptito, Weekes, & Zaidel, 2000; Miniussi, Girelli, & Marzi, 1998; Savazzi & Marzi, 2004).

Finally, the involvement of subcortical structures in emotional processing (like amygdale, colliculi, or striatum) suggests that interhemispheric cooperation for affective stimuli might be predominantly mediated by connections at the level of the limbic system. This hypothesis deserves further investigation through neuroimaging techniques or lesion studies, but seems intuitively supported by the fact that neural summation is generally stronger in split-brain than in normal subjects, therefore pointing to a subcortical contribution that is normally inhibited at the cortical level (Corballis, 1995, 1998; Corballis, Hamm, Barnett, & Corballis, 2002; Roser & Corballis, 2003).

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