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Hemispheric asymmetry in discriminating faces differing for featural or configural (second-order relations) aspects

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Running head: Hemispheric specialization in featural and relational processing of faces

Abstract

Human capacity to discriminate among different faces relies on distinct parallel sub-processes, either based on analysis of configural aspects of faces or on the sequential analysis of the single elements of a face. A particular type of configural processing consists in considering whether two faces differ in terms of internal spacing among their features, i.e., second-order relations processing. Findings from electrophysiological, neuroimaging and lesions' studies suggest that overall configural processes rely more on right hemisphere's resources, whereas analysis of single features would involve more the left hemisphere. However, results are not always consistent, and there is no yet clear behavioral demonstration for a right-hemisphere specialization in second-order relations processing. Here we used divided visual field presentation to investigate the possible different contribution of the two hemispheres in faces' discrimination based on relational vs. featural processing. Our data indicate a right hemisphere specialization in relational processing of upright (but not inverted) faces, and provide evidence on the involvement of both right and left hemisphere resources in processing faces differing for inner features, suggesting that in this case both analytical and configural modes of processing are at play.

Keywords: configural; featural; face processing; right hemisphere; lateralization; **divided visual field**; Jane faces task

Introduction

The ability that humans have to quickly detect faces among other objects and to discriminate among the multitude of different faces encountered in everyday life depends on several types of processing (see Cabeza & Kato, 2000; Carbon 2011; Maurer, Le Grand, & Mondloch, 2002; Leder & Carbon, 2006; Rotshtein, Geng, Driver, & Dolan, 2007; Schwaninger, Lobmaier, & Collishaw, 2002; Tanaka & Farah, 1993; Todorov, Loehr, & Oosterhof, 2010; Tsao & Livingstone, 2008). In particular, "first-order information" (i.e., the basic attributes present in each face, such as two eyes, a nose, a mouth) is used for "holistic" processing of a face, allowing one to quickly discriminate a face from a non-face stimulus (Maurer et al., 2002; McKone, Martini, & Nakayama, 2003). Furthermore, to discriminate among different faces, individuals rely on both 1) the analysis of single features within the face (such as the shape, colour or texture of the eyes or the nose), a type of encoding known as "featural processing", and 2) on processing of second-order configuration of these features (i.e., distance between the eyes, between the eyes and the mouth, etc) or "relational processing" (Maurer et al., 2002). Converging evidence collected in healthy adults and children, as well as in individuals affected by face recognition selective deficits such as congenital prosopoagnosia, suggests that featural and relational types of face processing rely on different, although strongly associated (see Yovel & Kanwisher, 2008), mechanisms (Freire, Lee, & Symons, 2000; Henderson, McCulloch, & Herbert, 2003; Leder & Carbon, 2006; Le Grand, Mondloch, Maurer, & Brent, 2003; Lobmaier, Bolte, Mast, & Dobel, 2010; Mondloch, Le Grand, & Maurer, 2002; Mondloch, Robbins, & Maurer, 2010; Rhodes, Hayward, & Winkler, 2006; Rotshtein, Geng, Driver, & Dolan, 2007; Xiao, Quinn, Ge, & Lee, 2012).

In fact, featural and relational processes (and also holistic processing of faces) are also likely to be mediated by different neural networks, involving the two hemispheres differently (e.g., Lobmaier et al., 2008; Maurer et al., 2007; Mercure, Dick, Johnson, 2008; Pitcher, Walsh, Yovel, & Duchaine, 2007; Rossion et al., 2000; Scott & Nelson, 2006). In particular, holistic processing and processing of second-order relations of faces are likely to be mainly mediated by the right hemisphere, whereas analysis of the single features is likely to mainly rely on the left hemisphere Results are not entirely consistent however. For instance, using the divided visual field methodology (in which stimuli are selectively presented in the left or right visual field, thus preferentially activating the contralateral hemisphere), Hillger and Koenig (1991) reported a right visual field/left-hemisphere advantage in a same-different judgment task for faces in which faces differed for a single feature (the same result was also reported by Parkin & Williamson, 1987). However, when faces differed for more than one feature, a right-hemisphere advantage was reported (Hillger & Koenig, 1991). Other studies using the divided visual field methodology to assess hemispheric specialization for holistic processing of faces have generally reported a left visual field/right hemisphere advantage (Ramon & Rossion, 2010; Parkin & Williamson, 1987). Although processing of second-order relations of faces has not been investigated so far through a divided visual field methodology, neuroimaging and electrophysiological evidence suggests that this type of processing taps more into the right hemisphere's resources (see Maurer et al, 2007; Scott & Nelson, 2006). In particular, fMRI evidence suggests a prevalent left-frontal hemisphere activation associated with featural processing, and a prevalent right fronto-parietal activation associated with processing of second-order relations of faces (Maurer et al., 2007; see also Lobmaier et al., 2008). ERPs evidence also indicates a major contribution of the left hemisphere in featural processing, and of the right hemisphere in relational processing of faces (Scott & Nelson, 2006). Nonetheless, using TMS, Pitcher et al. (2007) showed that a face-specific region in the right hemisphere, the occipital face area (rOFA), plays a critical role in processing face parts but not in processing the spacing between these parts. Furthermore, other neuroimaging studies failed to report a different activation in face-selective regions - such as the fusiform face area (FFA) - depending on detection of featural versus relational changes (Yovel & Kanwisher, 2004; see also Maurer et al., 2007; but see Rothstein et al., 2007).

In this study, we used lateralized stimulus presentation to investigate possible hemispheric differences in judging the identity of two consecutively presented faces differing for either featural or (second-order) configural aspects. This is particularly interesting since processing of second-order relations of faces has not been investigated so far through a divided visual field (DVF) methodology. The use of this method is also relevant in light of controversial results previously reported in the literature when investigating discrimination for faces differing for facial features (Hillger & Koenig, 1991; Maurer et al., 2007; Pitcher et al., 2007). To the purpose of our investigation, we used the so-called "Jane faces task" (Maurer et al., 2007; Mondloch et al., 2002), in which the same face (Jane) is modified to obtain eight different versions ("Jane's sisters"): four differing for single elements (the shape of eyes and the mouth; featural set) and four for spacing among the same facial elements (relational set). Notably, each set (featural and relational) was also presented with faces in an upside-down orientation. Although inversion impairs face discrimination overall, there is evidence that it

affects more detection of relational changes than of featural changes (e.g., Mondloch et al., 2002), particularly affecting a face-specific configural mode of processing (see also Le Grand et al., 2001, 2003; Robbins et al., 2010). With inverted faces this mechanism cannot be efficiently applied: accordingly, the inversion manipulation in our DVF experiment allows shedding further light on possible hemispheric asymmetry in the different mechanisms underlying face processing.

Method

Participants

Twenty students (5 males; mean age = 23.2 yrs, *SD*= 1.60; range: 19-27 yrs), all right handed (Oldfield, 1971), took part in the experiment. All had normal or corrected-to-normal vision. Written informed consent was obtained from all participants and the study was approved by the local ethical review committee.

Material and Procedure

Participants sat 57 cm from a 17″ computer monitor (1440 × 900; refresh rate: 60 Hz). A chin-rest was used to ensure that the head was aligned with the middle of the screen and that distance from the screen was kept constant. E-prime 2 (Psychology Software Tools, Pittsburgh, PA) was used for stimuli presentation and data collection.

Face stimuli (see Figure 1a) subtended 5° of visual angle in width and 8° of visual angle in height and consisted of gray-scale photographs (image resolution: 72 x 72 dpi) of a single Caucasian young female face (called “Jane”) and in its “featural” and “relational” variants (“Jane’s sisters”) (see Mondloch et al., 2002, for details). In particular, four featural-different variants were created by replacing the original Jane face’s eyes and mouth with the features of the same length from different females. Four relational-different variants were created by moving the eyes of the original Jane up or down, closer together or farther apart, and the mouth up or down. The featural and relational sets were presented in separate blocks to allow time for each style of processing to emerge but participants were not explicitly informed about the distinctions (see Maurer et al., 2007). Each set was presented both with faces appearing in the standard upright orientation, and with faces appearing upside-down (inverted orientation). The inverted set was always presented after the upright set.

A divided visual field (DVF) paradigm was used (following criteria recommended by Bourne, 2006). The timeline of an experimental trial is presented in Figure 1b. Each trial started with a 1000 ms long central fixation cross, followed by the probe face which appeared in the middle of the screen for 150 ms in the featural set (the same duration was also used in the DVF study by Hillger and Koenig, 1991, with faces differing for single or multiple features) and for 180 ms in the relational set.[1] A central fixation cross was then presented. After 500 ms since the onset of the fixation cross, the target face was presented for 150 ms in the featural set and for 180 ms in the relational set, the inner border of the laterally presented face being located either 3° to the left or 3° to the right of the fixation cross (see Bourne, 2006). The central fixation cross remained visible till participants' response. The following trial was initiated by participants' response. Participants responded with left/right key pressing (response key assignment was counterbalanced across participants) using their left and right index finger, and were instructed to maintain fixation on the central fixation cross while performing the task. In each block (featural upright, featural inverted, relational upright, relational inverted), all the possible pair-combinations of Jane and its four variants were presented in random order, with each face appearing an equal number of times in the left and in the right hemifield. Each block consisted of 160 trials (80 "different" trials and 80 "same" trials); each face appeared an equal number of times as probe and target face, and an equal number of times in the left and right visual field. Participants could take short breaks during the experiment.

[insert Figure 1 about here]

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[1] A longer presentation duration was decided for the relational set to avoid floor effects with inverted faces (note that accuracy in the inverted relational set was slightly above chance, but we preferred not to further increase duration in order to avoid eye movements, see Bourne, 2006, p. 381: " […] it is recommended that stimulus presentation is limited to a maximum exposure of 180 ms, with exposure ideally limited to 150 ms if the task is a simple one").

Before the experiment, a short slide presentation was shown to explain the task. The difference or identity between stimuli was emphasized, but no explicit cues were provided on the type of changes that could occur. Further, prior to the task, short practice blocks for each set and orientation were performed in order to familiarize participants with the task. Response speed was encouraged in addition to accuracy**. The importance of maintaining fixation in the center of the screen was stressed throughout the task. The whole experiment lasted approximately 1 hour.**

Analyses

Mean accuracy and mean reaction times (RT) since onset of the target face for correct responses were computed individually per condition. Trials in which individual response latencies were beyond 3 standard deviations with respect to each participant's mean performance in each experimental block were excluded from the analyses (following this criterion, a total of 1.46% trials were overall excluded). Importantly, further analyses were performed on the d' prime and the response bias (*c*) measures (see MacMillan and Creelman, 1991), in light of previous evidence (cf. Hillger & Koenig, 1991) suggesting that hemispheric asymmetry in processing faces may be different depending on type of trial ("same" and "different" trials). Moreover, RTs adjusted for level of accuracy (mean RT/ACC, also known as "inverse efficiency scores", see Townsend & Ashby, 1978) were considered, to rule our possible speed-accuracy trade –off (see also Ramon & Rossion, 2012). The response key assignment was also considered in light of previous evidence showing the occurrence of Simon-like effects in DVF paradigms (see Bourne, 2006) and possible interactions with visual field's effects in face processing (Hillger & Koenig, 1991). Finally, although there is evidence for different degrees of hemispheric lateralization in male and female individuals (e.g., Hiscock et al., 1995, for a review), the effect of sex was outside the focus of this work and was therefore not considered (see also Ramon & Rossion, 2012).

A repeated measures ANOVA with orientation (upright faces vs. inverted faces) and visual field (VF; left vs. right) as within-subjects variables and response key assignment as between-subjects variable was carried out for all the considered dependent variables for the featural and the relational set separately.

Results

Relational set

Mean accuracy: Mean accuracy as a function of VF and experimental condition is reported in Figure 2a. The ANOVA on mean accuracy showed a significant main effect of orientation, $F(1,18)=59.93$, $p<.001$, $\eta_p^2=.77$, due to accuracy being higher overall with upright than with upside-down faces. The main effect of VF was significant, $F(1,18)= 7.47$, $p=.014$, $\eta_p^2=.29$, with accuracy being higher in the left than in the right visual field. No significant main effect of response key assignment was observed ($p=.396$). Critically, the effect of VF depended on face orientation, as demonstrated by the (almost) significant interaction VF by orientation, $F(1,18)= 4.35$, $p=.052$, $\eta_p^2=.20$. Post-hoc comparisons indicated that when faces were presented in the standard upright orientation, accuracy was significantly higher when the target face appeared in the left than in the right visual field, $t(19)=3.13$, $p=.005$. Conversely, no differences related to VF were overall observed for faces presented upside-down, $t(19)=.72$, $p=.480$. None of the remaining interactions reached significance (all *ps*>.19).

d' prime: The same pattern of results as that obtained with accuracy as dependent variable was obtained when considering d' prime (see Figure 2b). Also in this case, the ANOVA reveled a significant main effect of orientation, $F(1,18)=54.86$, $p<.001$, $\eta_p^2=.75$, with upright faces being discriminated better than upside-down faces. Detection of differences was significantly higher in the left than in the right VF, $F(1,18)= 6.51$, $p=.020$, $\eta_p^2=.27$, but also in this case the effect depended on face orientation, as suggested by the significant interaction VF by orientation, $F(1,18)= 4.97$, $p=.039$, $\eta_p^2=.22$. Post-hoc comparisons confirmed that d' prime was higher in the left than in the right VF for upright faces, $t(19)=2.98$, $p=.008$. Conversely, no differences related to VF were overall observed for faces presented upside-down, $t(19)<1$, $p=.530$. No main effect of response key assignment was observed ($p=.617$). None of the remaining interactions reached significance (all *ps*>.10).

[Insert Figure 2 about here]

Mean correct RT and IE scores: Mean correct reaction times as a function of VF and orientation are shown in Figure 3a. The ANOVA did not reveal any significant main effect for VF (*p*=. 442) or orientation (*p*=.92). The effect of response assignment was not significant (*p*=.717). None of the interactions reached significance (all *ps*>.40). Mean participants' adjusted RT (IE scores) are shown in Figure 3b. Although the pattern of performance reflected that found when accuracy and d' measures were considered, the ANOVA only revealed a significant effect of orientation, *F*(1,18)= 10.39, *p*=.005, η_p^2=.37, reflecting higher difficulty in discriminating inverted than upright faces. The main effect of VF was not significant (*p*=.208). The effect of response assignment was not significant (*p*=.567). None of the interactions reached significance (all *ps*>.09).

[Insert Figure 3 about here]

Response bias (c): Figure 4 shows participants response bias as a function of orientation, VF and response key assignment. The ANOVA revealed a significant effect of orientation, *F*(1,18)=12.78, *p*=.002, η_p^2=.42, and a significant interaction orientation by VF by response key assignment, *F*(1,18)=5.14, *p*=.036, η_p^2=.22. Neither the main effect of VF (*p*=.128) nor the main effect of response key (*p*=.318) nor any of the other possible interactions (all *ps*>.22) reached significance. The significant effect of orientation depended on a overall greater tendency to respond "different" than "same" with inverted faces: in other words, although participants tended overall to be more liberal than conservative (*c* values being negative for both upright and inverted faces, indicating that number of false alarms exceeded number of misses), they were nonetheless significantly more conservative in their judgment when faces appeared in the standard upright orientation. However, this was modulated by response key and VF (see Figure 4b). When faces appeared in the right VF the tendency to respond "different " was comparable for upright and inverted faces regardless of response key (*p*=.367 for the left-key meaning "different" ; *p*=.286 for the right-key meaning "different"). When target faces were presented in the left VF: 1) participants pressing the left key to respond "different" showed a higher "different" bias with inverted than with upright faces, *t*(9)=2.12, *p*=.063; 2) participants pressing the right key to respond "different" showed a slight "different" bias with upright faces, but a slight "same" bias (positive c) with inverted faces, although these two opposite tendencies did not significantly differ, *t*(9)=1.84, *p*=.099.

[Insert Figure 4 about here]

Featural set

Mean accuracy: Mean accuracy for upright and inverted faces differing for facial inner features is presented in Figure 5a. The ANOVA revealed a significant main effect of orientation, $F(1,18)=66.60, p<.001, \eta_p^2=.79$, due to accuracy being higher with upright than with inverted faces. Neither the main effect of VF ($p=.821$) nor the main effect of response key assignment was significant ($p=.452$). Two interactions were significant: the two-ways interaction VF by orientation, $F(1,18)= 7.36, p=.014, \eta_p^2=.29$, and the three-ways interaction VF by orientation by response key, $F(1,18)= 4.43, p=.050, \eta_p^2=.20$. None of the remaining interactions reached significance (all *ps*>.80). As shown in Figure 5a, the interaction VF by orientation resulted from participants tending to discriminate better (but not to a significant extent) upright faces when presented in the left VF, $t(19)=1.37, p=.185$, whereas with inverted faces a slight not significant advantage emerged for the right VF, $t(19)=2.54, p=.272$. Critically though, this pattern was evident only in participants using the left key to respond "different", whereas for the opposite response key assignment no trend of hemispheric asymmetry emerged (see Figure 5b).

[Insert Figure 5 about here]

d' prime: d' prime scores are reported in Figure 5c. The analysis revealed a significant main effect of orientation, $F(1,18)=73.63, p<.001, \eta_p^2=.80$, indicating better discrimination of upright faces than upside-down faces. Neither the main effect of VF ($p=.768$) nor the main effect of response key ($p=.330$) were significant. None of the interactions reached significance. Although the interaction visual field by orientation failed to reach significance ($p=.147$), d' prime scores showed a similar pattern as accuracy scores with better discrimination capacity in the left VF than in the right VF with upright faces only (a tendency toward a right VF advantage was observed for upside-down faces). The interaction VF by orientation by response key that in case of accuracy was significant, only approached significance here (p=.077): as in case of accuracy the left VF advantage for upright faces was more evident in participants pressing the left key than in those pressing the right key to respond "different" .

Mean correct RT and IE scores: Figure 6a shows mean correct reaction times as a function of VF and for the featural set. The ANOVA revealed a significant main effect of orientation, $F(1,18)=13.82, p=.002, \eta_p^2=.43$, a significant main effect of response key, $F(1,18)=9.31, p=.001, \eta_p^2=.34$, and a significant interaction between orientation and response key, $F(1,18)=26.97, p<.001, \eta_p^2=.60$. The main effect of VF was not significant (p=.730). None of the other interactions reached significance (all *ps*>.36). Participants pressing the left key to respond "different" were overall slower (mean RT= 993 msec) than those pressing the right key to respond "different" (mean RT=769 msec). The significant main effect of orientation depended on participants being overall slower in discriminating upright than inverted faces, an effect though that was driven by participants using the left key to respond "different" (p>.001, inverted faces advantage = 129 msec), since participants using the right key were slightly faster with upright than with inverted faces (p=.336, upright faces advantage = 22 msec). Analysis on the IE scores (Figure 6b) confirmed that the overall faster RT with inverted faces depended on speed-accuracy trade-off. In fact, the analysis on IE scores showed a significant effect of orientation, $F(1,18)=22.17, p<.001, \eta_p^2=.55$, indicating higher difficulty in discriminating inverted than upright faces. The main effect of VF was not significant (p=.919). Critically, the interactions VF by orientation, $F(1,18)=6.35, p=.021, \eta_p^2=.26$, and VF by orientation by response key, $F(1,18)=5.29, p=.034, \eta_p^2=.23$, were significant, reflecting the pattern found with accuracy scores (see above). Response key assignment, $F(1,18)=7.77, p=.012, \eta_p^2=.301$, and the interaction response key by orientation, $F(1,18)=5.60, p=.029, \eta_p^2=.24$, were significant: these effects were driven by RT *per se* (see above) and reflected longer RT in participants using the left key to respond different, and a less evident advantage in processing upright over inverted faces in this group.

[Insert Figure 6 about here]

Response bias (c): Figure 7 shows participants' response bias for upright and inverted faces in the left and right VF and as a function on response key assignment. The ANOVA revealed a significant effect of orientation, $F(1,18)=7.67$, $p=.013$, $\eta_p^2=.30$, and a significant main effect of VF, $F(1,18)=6.62$, $p=.019$, $\eta_p^2=.27$. The main effect of response key was not significant ($p=.802$). The interaction orientation by response key approached significance, $F(1,18)=4.17$, $p=.056$, $\eta_p^2=.19$. None of the other possible interactions (all *ps*>.374) reached significance. Participants were overall more keen on responding "different" than on responding "same" (negative *c*): this bias toward "different" was more evident in the right than in the left VF, and greater for inverted than for upright faces (the stronger "different " bias with inverted than upright faces was more evident in participants pressing the left key to respond "different").

[Insert Figure 5 about here]

Discussion

In this study we used a divided visual field paradigm to investigate possible hemispheric asymmetries in discriminating among faces differing for either second-order configural changes or facial features and presented either in a standard upright orientation or inverted (i.e., upside-down).

Discrimination of faces differing for second-order configural changes has never been investigated before using a DVF methodology. Our findings showed an overall left VF/right hemisphere accuracy advantage in discriminating upright faces differing for spacing among otherwise identical features (relational set). The same pattern was obtained when consider signal detection sensitivity (d', see MacMillan and Creelman, 1991). The convergence in results we got between the accuracy and the d' scores is critical, given previous evidence indicating that the type of trial ("same" vs. "different") may interact with hemispheric asymmetry (e.g., Hillger & Koenig, 1991). The d', by inherently considering the type of trials in a unique measure, confirmed a robust right hemisphere advantage in discriminating upright faces in the relational set. Performance was overall higher for upright than for inverted faces, an advantage that was not affected by the visual field manipulation. The same trend in performance was found when considering inverse efficiency scores (RT/accuracy, Townsend & Ashby, 1978) ruling out possible effects of speed-accuracy trade-offs in driving accuracy scores.

The left VF/right hemisphere advantage found for relational processing of upright faces corroborate previous neuroimaging and ERPs evidence indicating a right-hemisphere specialization in discriminating faces based on differences in their second-order relations (Maurer et al., 2007; Scott & Nelson, 2006). The absence of a left visual field advantage with inverted faces is also consistent with previous evidence indicating that inversion affects face discrimination, interfering more with holistic processing of faces (i.e., perceiving a face as a gestalt) and relational processing of faces (i.e., processing of the spatial links among facial features), compared to featural processing of faces (cf. Carbon & Leder, 2005; Leder & Bruce, 2000; Leder & Carbon, 2006; McKone & Yovel, 2009; Rakover, 2012). As also suggested by prior findings collected with cataract reversal patients using the same faces set used here (Le Grand et al., 2001, 2003; Robbins et al., 2010), inversion is likely to disrupt a configural mode of processing that seems to be specific for human faces presented in their standard upright faces, and that is not employed in processing other animal faces (as monkeys) or objects (a houses). When the configural mode of encoding is prevented by inversion, the role of the right hemisphere becomes less prominent, in agreement with our results.

Notably, we did not find evidence for a clear hemispheric asymmetry when considering discrimination of faces differing for inner features (i.e., mouth and eyes). In fact, all the relevant measures considered (accuracy, d' and inverse efficiency scores) consistently indicated a different trend in hemispheric asymmetry for upright and inverted faces depending on VF: a slight left VF advantage for upright faces, and a slight right VF advantage for inverted faces. However, for none of these categories (upright and inverted faces) the effect of VF reached full significance. Previous fMRI and ERPs evidence have suggested a more prominent role of the left hemisphere compared to the right hemisphere in encoding featural aspects of faces (Maurer et al., 2007; Scott & Nelson, 2006). However, a left-hemisphere preference for featural processing vs. second-order relational processing has not been replicated in other fMRI and ERPs studies (e.g., Mercure et al., 2007; Rotshtein et al., 2007). In considering our findings in the featural set, it is important to note that changing featural elements of a face inherently implies also a change in the resulting face configuration. Hence, configural processing is also involved in discriminating upright faces differing for inner features. In this respect, the results obtained by Hillger and Koenig (1991) are critical: using a DVF paradigm, the authors reported a right-hemisphere advantage for upright faces differing for multiple features (i.e., changes simultaneously affecting the eyes, the nose, and the mouth). However, when faces differed for only one facial feature a more complex pattern emerged: when faces were identical ("same" trials), a left VF/right hemisphere advantage was found (but this advantage disappeared when faces were presented upside-down in a further experiment); when faces differed ("different" trials), a left hemisphere/right VF advantage emerged (that was still evident when faces were presented upside-down). According to Hillger and Koenig (1991) these findings provide evidence for the existence of a face-specific holistic process in discriminating upright faces that would be mainly mediated by the right hemisphere, and that would be disrupted by inversion; and for the existence of a more general (not face-specific) visual analytic process responsible for detection of single local changes mainly mediated by the left hemisphere and not affected by inversion. The extent to which configural and analytical processes are at play likely depend on the number of features that simultaneously change and on their salience (see Hillger & Koenig, 1991). In our featural set, faces differ for the mouth and the eyes simultaneously. Our situation was thus intermediate between the single-feature and the three features' changes used by Hillger and Koenig (1991). Our data seem to indicate that with upright faces a configural mode of processing was playing a major role (trend toward an advantage for left VF/right hemisphere) advantage. When this configural processing was blocked by inversion, participants could still rely on analytical mode of processing as reflected by a slight advantage for right VF/left hemisphere presentation (with this analytical mode of processing being of no help in case of spacing changes, see above).

The visual field's effects we reported in our experiment were visible for accuracy scores but not for reaction times. Accordingly, several previous studies employing a sequential same-different face matching task investigating featural vs. spacing processing have selectively reported effects of experimental manipulations on accuracy (e.g., Keyes, 2012; Lobmaier et al., 2010; Pitcher et al., 2007; Rakover, 2012; Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Yovel & Kanwisher, 2008), suggesting that reaction times may be a less sensitive measure than accuracy in this kind of tasks. Moreover, speed-accuracy trade-offs need to be considered: in this respect, a more adequate measure consists in the "inverted efficiency" scores in which RT are adjusted for accuracy (see also Ramon & Rossion, 2012). When considering this variable in our analyses, the pattern of results mirrored those obtained with accuracy for both the featural and the relational set (although failing to reach full significance).

In our analyses we also considered possible effects due to pre-existing response bias (i.e., individual "a priori" tendency to respond "different" or "same", see MacMillan and Creelman, 1991) and possible effects related to response key assignment (as recommended by Bourne, 2006). With regard to response bias, our participants tended to be overall more "liberal" than conservative, tending to respond "different" more often than "same" (i.e., the number of false alarms was greater than number of misses). This was especially evident in both the relational and the featural sets with inverted faces, whereas with upright faces participants tended to be slightly more conservative (although the number of false alarms was still greater than number of misses). Moreover, the "different" bias was more evident for faces appearing in the right VF than in left VF (this difference reaching significance only in the featural set). Overall, these results indicate that when level of uncertainty was greater, the "a prior" response bias became stronger. Notably, response bias interacted with response key assignment. The pattern of interactions was quite complex, the main finding being that higher "different" bias with inverted than upright faces was particularly evident in participants using the left key to respond "different". These effects may be at least partially accounted for by the existence of a preferential mapping between "different response" and left hand and "same response" and right hand, also reported in previous studies (Hillger and Koeing, 1991), with the "different" bias becoming more prominent in uncertain decisions especially for participants with a congruent mapping between type of response (different) and hand used to respond (left). Response key assignment also affected discrimination of faces in the featural set. In particular, hemispheric asymmetry (a slight trend toward better discrimination for upright faces in the left VF and inverted faces in the right VF) was mainly driven by participants using the left key to respond different (preferred type of response-hand mapping, see above). Similar results were also obtained by Hillger and Koenig (1991) and are likely to indicate that effects of hemispheric asymmetry are overall more visible when the preferential mapping of response key and type of response is used (i.e., left key for "different" responses).

In sum, our results provide a straightforward behavioral demonstration of a right hemisphere specialization in relational processing of upright faces, extending previous evidence obtained with fMRI and ERPs methodologies (e.g., Maurer et al., 2007; Scott & Nelson, 2006), and adding to previous behavioral data obtained in divided visual fields paradigms testing featural vs. holistic (but not specifically relational-based) processing of faces. Our data also provide evidence on the involvement of both right and left hemisphere resources in processing faces differing for inner features, suggesting that in this case both analytical and configural modes of processing are at play.

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Figure legends.

Figure 1. A) The Jane original face and her "sisters" differing for changes in single features or for the spacing (relational changes) among the face's elements. **B)** The timeline of an experimental trial. Participants had to indicate whether the two faces were identical or not and were instructed to be both accurate and fast.

Figure 2. A) Participants' mean accuracy and **B)** detection sensitivity (d') in the *relational set* of the Jane faces task for upright and inverted faces as function of VF. Performance was significantly higher for upright faces appearing in the left VF. Error bars represent ±1 SEM. Asterisks indicate a significant difference between the two VFs.

Figure 3. A) Participants' mean correct response latencies and **B)** mean participants' response latencies adjusted for accuracy (inverse efficiency scores) in the *relational set* for upright and inverted faces as function of VF. Error bars represent ±1 SEM.

Figure 4. A) Participants' mean response bias in the *relational set* for upright and inverted faces as function of VF, and **B)** as a function of response key assignment. Error bars represent ±1 SEM.

Figure 5. A) Participants' mean accuracy in the *featural set* of the Jane faces task for upright and inverted faces as function of VF and **B)** as a function of response key assignment. **C)** Participants' mean detection sensitivity (d') in the different conditions of the *featural set*. Error bars represent ±1 SEM.

Figure 6. A) Participants' mean correct response latencies and **B)** mean participants' response inverse efficiency scores in the *featural set* for upright and inverted faces as function of VF. Error bars represent ±1 SEM.

Figure 7. A) Participants' mean response bias in the *featural set* for upright and inverted faces as function of VF, and **B)** as a function of response key assignment. Error bars represent ±1 SEM.

Figure 1

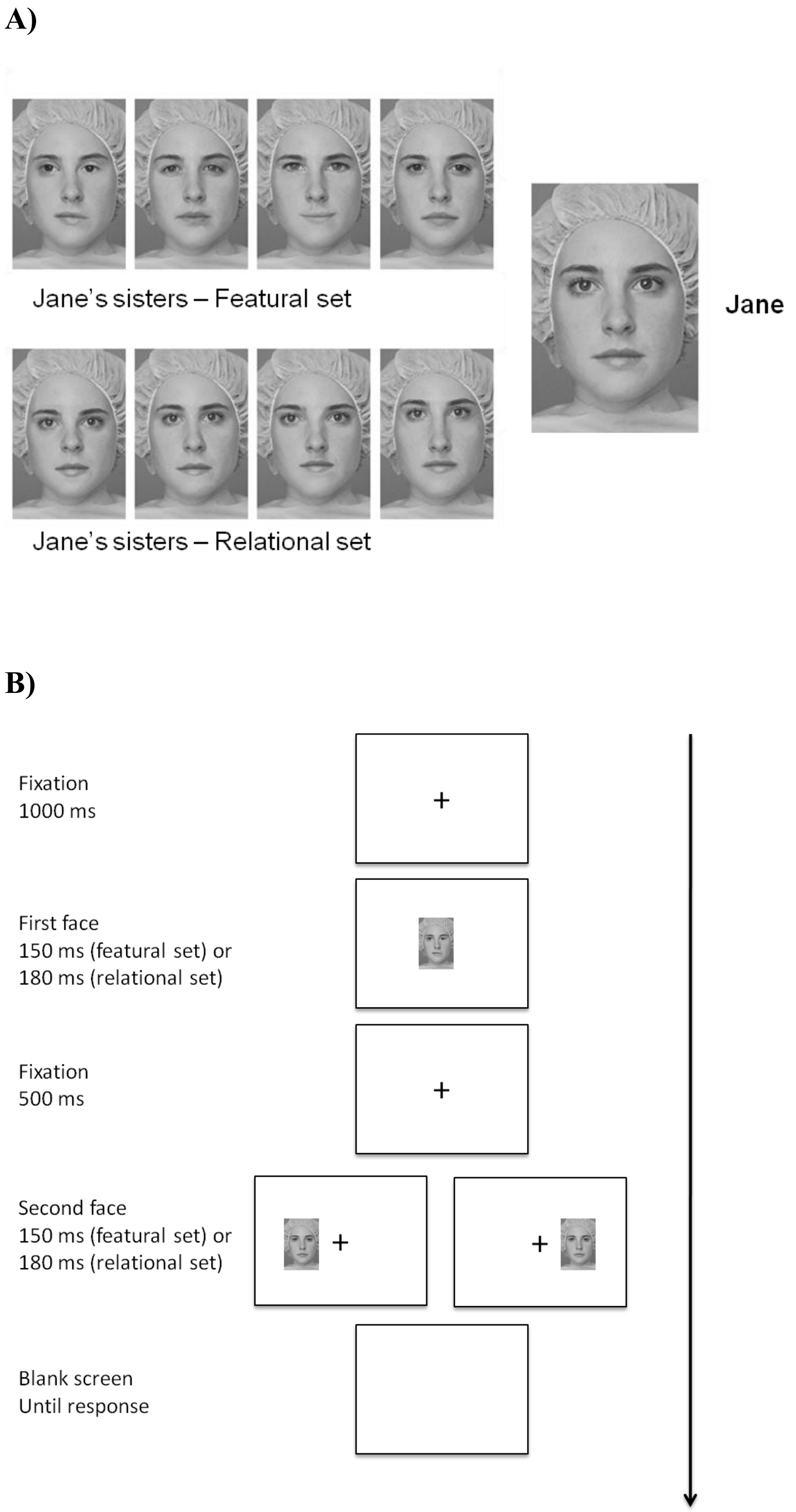

A)
Jane's sisters – Featural set
Jane's sisters – Relational set
Jane
B)
Fixation
1000 ms
+
First face
150 ms (featural set) or
180 ms (relational set)
Fixation
500 ms
+
Second face
150 ms (featural set) or
180 ms (relational set)
+
+
Blank screen
Until response

Figure 2

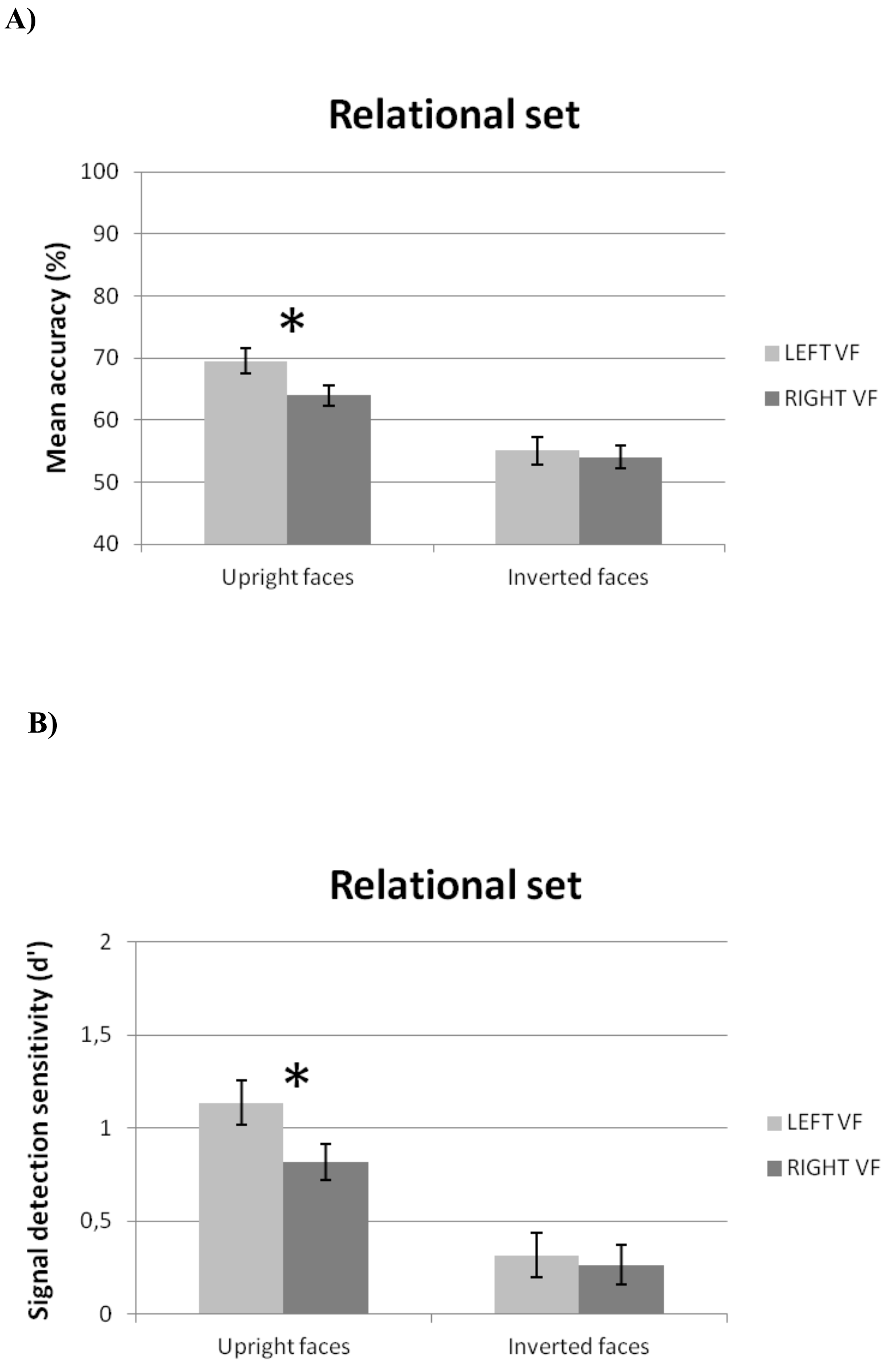
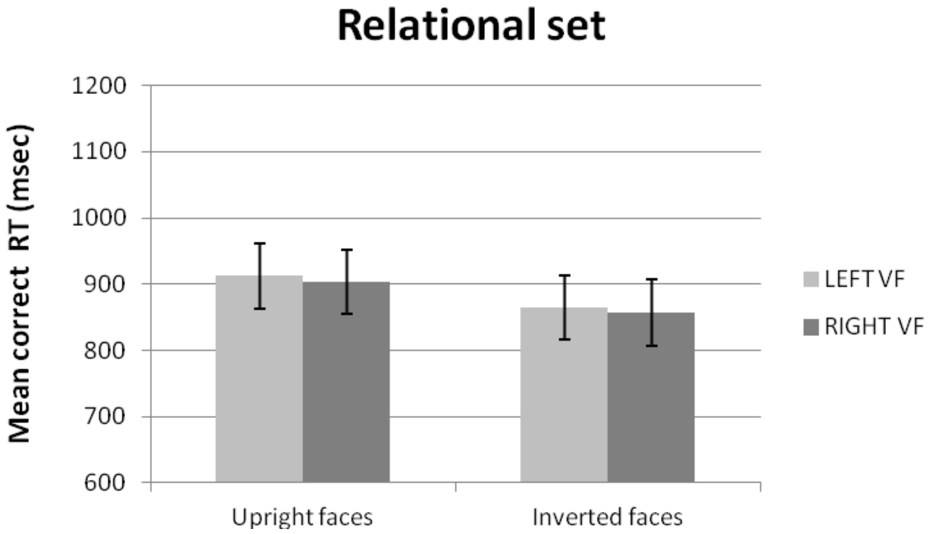

A)
Relational set
Mean accuracy (%)
100
90
80
70
60
50
40
*
Upright faces
Inverted faces
LEFT VF
RIGHT VF
B)
Relational set
Signal detection sensitivity (d')
2
1,5
1
0,5
0
*
Upright faces
Inverted faces
LEFT VF
RIGHT VF

Figure 3

A)


Relational set
Mean correct RT (msec)
1200
1100
1000
900
800
700
600
Upright faces
Inverted faces
LEFT VF
RIGHT VF

B)

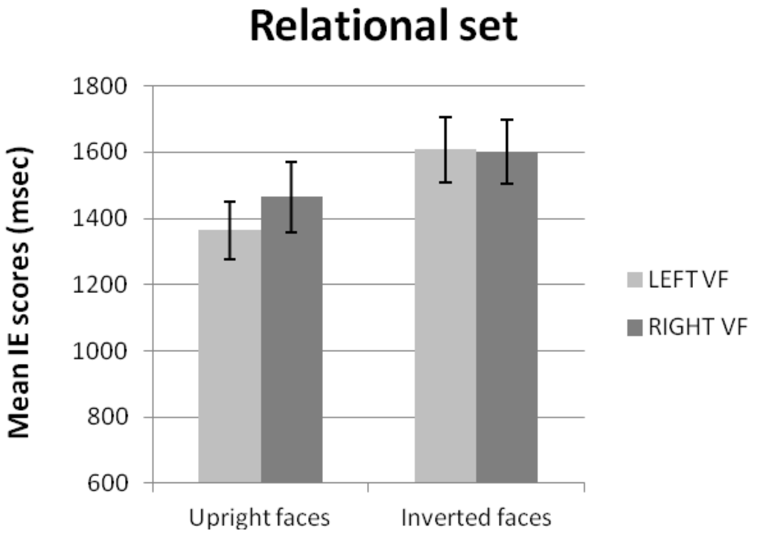
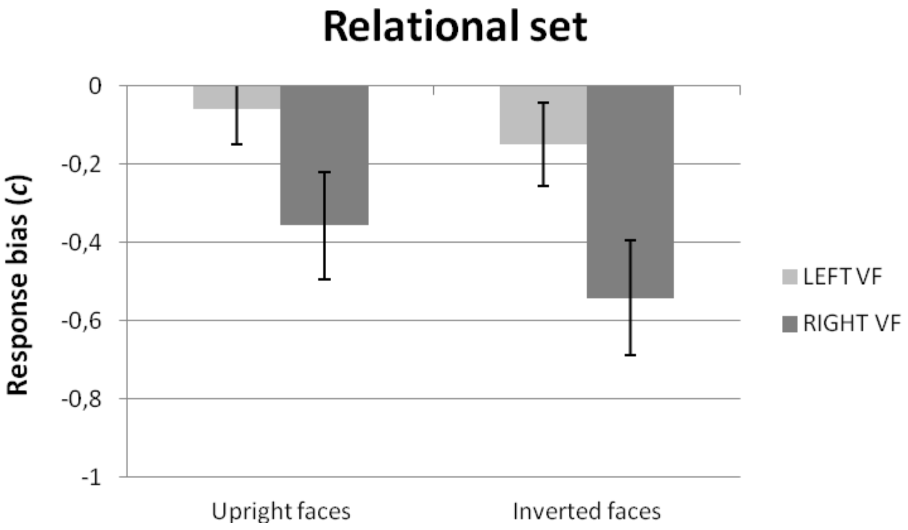

Relational set
Mean IE scores (msec)
1800
1600
1400
1200
1000
800
600
Upright faces
Inverted faces
LEFT VF
RIGHT VF

Figure 4

A)


Relational set
Response bias (c)
0
-0,2
-0,4
-0,6
-0,8
-1
Upright faces
Inverted faces
LEFT VF
RIGHT VF

B)

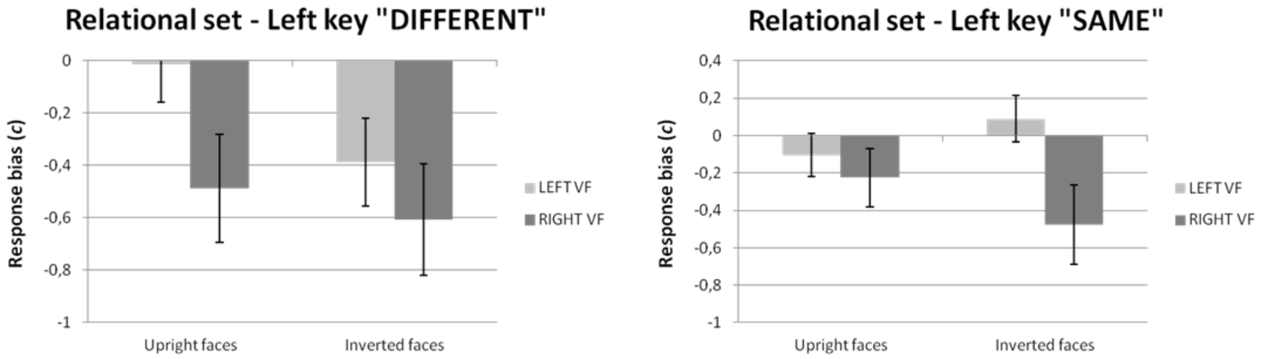

Relational set - Left key "DIFFERENT"
Response bias (c)
0
-0,2
-0,4
-0,6
-0,8
-1
Upright faces
Inverted faces
LEFT VF
RIGHT VF
Relational set - Left key "SAME"
Response bias (c)
0,4
0,2
0
-0,2
-0,4
-0,6
-0,8
-1
Upright faces
Inverted faces
LEFT VF
RIGHT VF

Figure 5

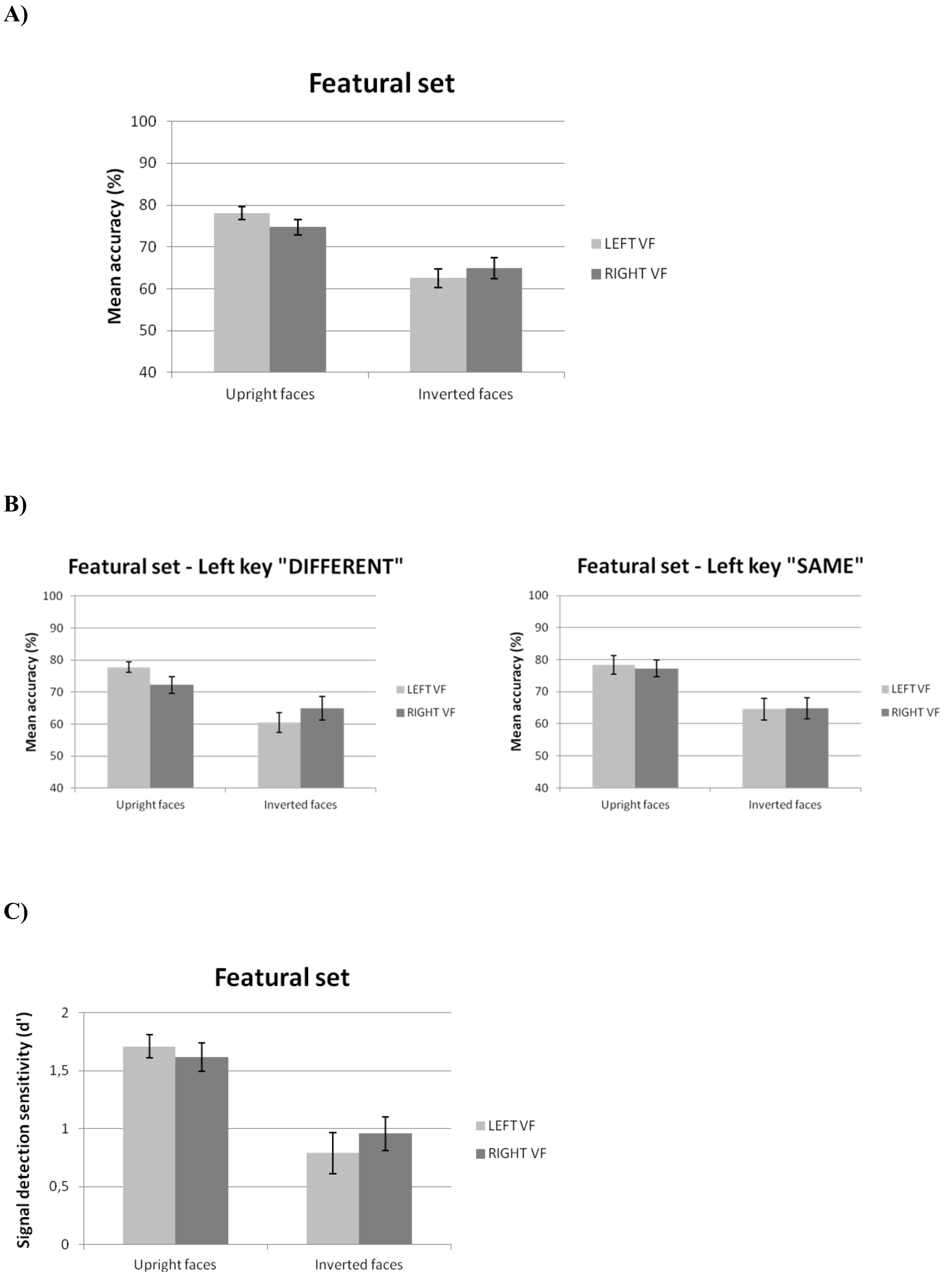
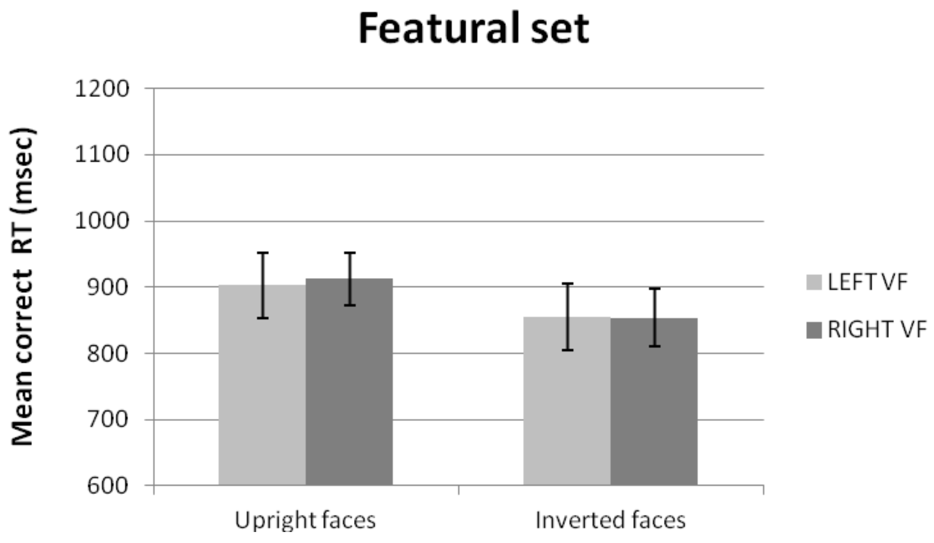

A)
Featural set
Mean accuracy (%)
100
90
80
70
60
50
40
Upright faces
Inverted faces
LEFT VF
RIGHT VF
B)
Featural set - Left key "DIFFERENT"
Mean accuracy (%)
100
90
80
70
60
50
40
Upright faces
Inverted faces
LEFT VF
RIGHT VF
Featural set - Left key "SAME"
Mean accuracy (%)
100
90
80
70
60
50
40
Upright faces
Inverted faces
LEFT VF
RIGHT VF
C)
Featural set
Signal detection sensitivity (d')
2
1,5
1
0,5
0
Upright faces
Inverted faces
LEFT VF
RIGHT VF

Figure 6

A)


Featural set
Mean correct RT (msec)
1200
1100
1000
900
800
700
600
Upright faces
Inverted faces
LEFT VF
RIGHT VF

B)

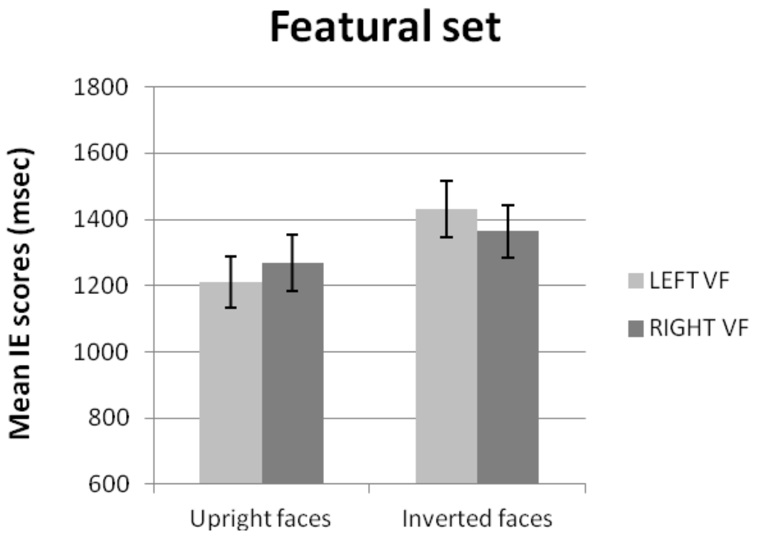
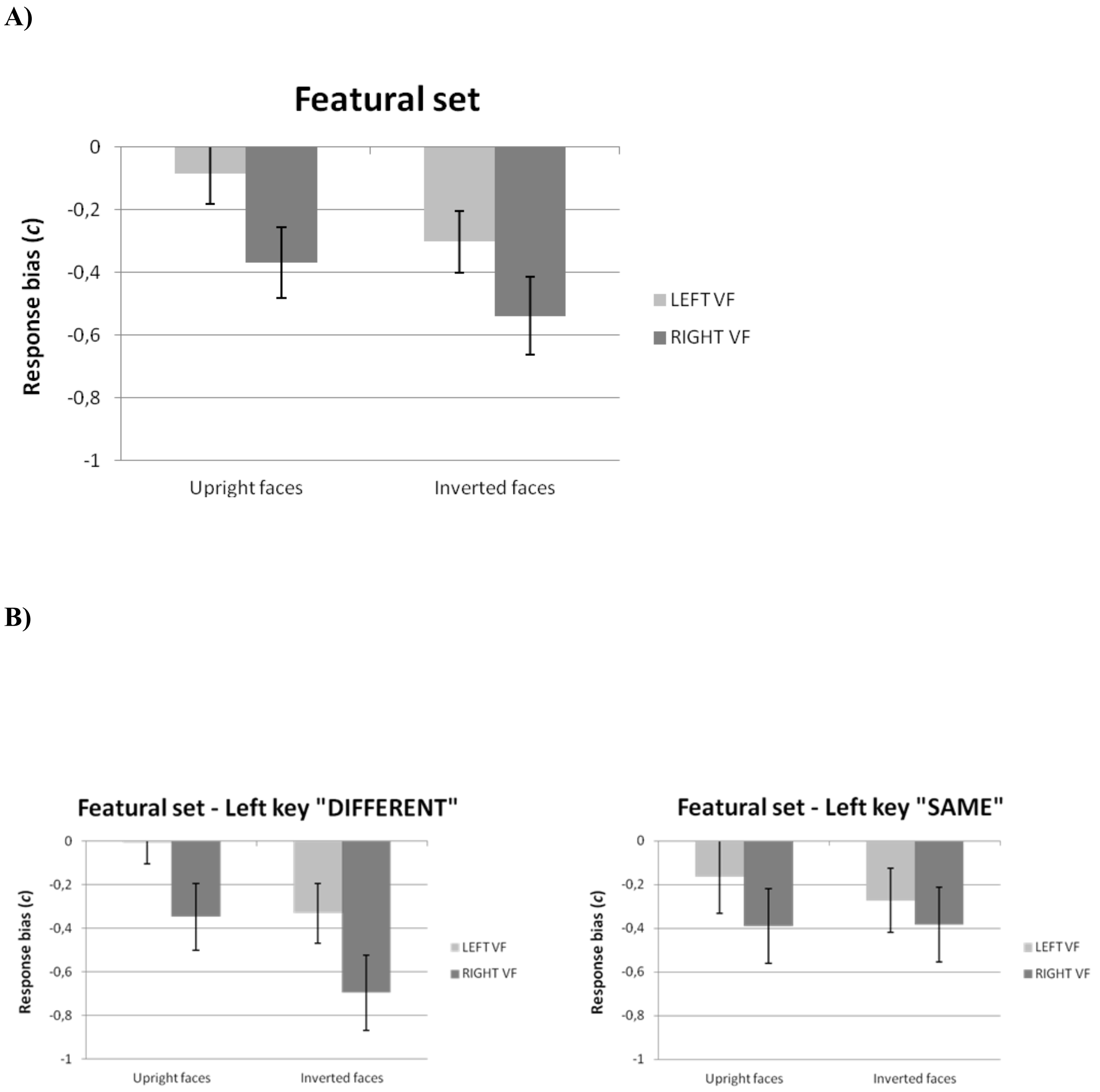

Featural set
Mean IE scores (msec)
1800
1600
1400
1200
1000
800
600
Upright faces
Inverted faces
LEFT VF
RIGHT VF

Figure 7


A)
Featural set
Response bias (c)
0
-0,2
-0,4
-0,6
-0,8
-1
Upright faces
Inverted faces
LEFT VF
RIGHT VF
B)
Featural set - Left key "DIFFERENT"
Response bias (c)
0
-0,2
-0,4
-0,6
-0,8
-1
Upright faces
Inverted faces
LEFT VF
RIGHT VF
Featural set - Left key "SAME"
Response bias (c)
0
-0,2
-0,4
-0,6
-0,8
-1
Upright faces
Inverted faces
LEFT VF
RIGHT VF

Acknowledgments

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