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Featural and configural face processing differentially modulate ERP components

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ABSTRACT

Since all faces share the same first-order configuration, individual faces are recognized by subtle differences in their individual features and second-order configuration. This study asked two questions about the ERP signatures of featural and configural face processing. First, which ERP components are sensitive to subtle modifications of features and second-order configuration? Secondly, does explicitly instructing participants to attend to either the features or the configuration of face stimuli influence the neural processes elicited by these stimuli? In the first part of this experiment, pairs of faces with differences in their features, in their second-order configuration or no difference were presented, with participants making same/different judgments. In the second part, participants were asked to focus on either the features or configuration in pairs of faces and to judge if there was any difference in that aspect while ignoring other differences. The P1 and N170 ERP components were not influenced by feature or second-order configuration differences in faces, indicating that these components could be more sensitive to manipulations that disrupt the first-order configuration of a face. In contrast, the P2 was larger in amplitude for faces with a configuration modification than for faces with a feature modification or for the original face. One explanation of these results is that processing the configuration of a face elicits more visual cortical feedback than processing the features. Finally, modulation of the P300 confirmed that the tasks presented in Part 2 were successful in varying the attention focus on the features or configuration.

1. Introduction

Since all faces share the same *first-order configuration* (two eyes above a nose above a mouth), the discrimination and identification of individual faces is based on the processing of *individual features* (shape of the eyes, nose and mouth) and on the processing of the *second-order configuration* of these features (the distance between the eyes, or between the mouth and nose, etc.) (Maurer et al., 2002). Understanding how the event-related potentials (ERPs) are influenced by subtle differences in face features or configuration could help understand the typical time course of face processing, and especially how individual faces are discriminated and identified.

The P1 component is usually thought to be mainly influenced by basic visual parameters such as luminance and contrasts, by the direction of spatial attention or by the participant's state of arousal (Luck, 2005). However, there is also evidence that this early component is sensitive to violations of the first-order configuration of a face. For

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example, Boutsen et al. (2006) observed that 'thatcherization' (inversion of the eyes and mouth relative to the rest of the face) increased the amplitude of the P1 component. Macchi Cassia et al. (2006) scrambled faces along two spatial dimensions: vertical symmetry (the symmetry of the left and right halves of a face along a vertical axis) and up–down featural arrangement (the proportion of high-contrast features in the upper compared to the lower part of the face). They observed that asymmetrical faces elicited a larger P1 compared to symmetrical faces, and that the P1 was larger when the eyes were presented in the bottom half of faces (bottom-heavy) than when they were presented in the top half of faces (top-heavy). However, are these early processes affected when faces retain their natural first-order configuration? Is the P1 sensitive to these more subtle differences of the second-order configuration or of the features that make discrimination of individual faces possible? Halit et al. (2000) found that elongating faces by increasing the eyes–nose–mouth distance influenced the P1 amplitude. Moreover, the P1 was larger for natural faces judged as atypical relative to natural faces judged as more typical. In sum, the literature suggests that the P1 may index functions beyond the low-level processing of visual stimuli and might be sensitive to the first- and second-order configuration of a face. It is not clear if this component is also affected by modifications of face features.

It is well-established that the N170 component is modulated by face processing. Specifically, this component is larger when elicited by human faces than by other object categories (Bentin et al., 1996). The N170 is not affected by stimulus familiarity, and is therefore more likely to reflect structural encoding of face stimuli rather than identity recognition (Bentin and Deouell, 2000; Eimer, 2000). However, it remains unclear what exactly is encoded at the stage of the N170. There is some evidence that the N170 could be sensitive to the processing of the eye features in a face. Using the 'Bubbles technique', Schyns et al. (2003) observed that a larger N170 amplitude was associated with the availability of eye information. Moreover, Bentin et al. (2002) observed that pairs of abstract patterns elicited an N170 similar to that of faces when they were perceived as eyes, but an N170 similar to that of objects when they were not perceived as eyes. Previous literature also suggests that the N170 component is sensitive to the first-order configuration of a face. Indeed, Boutsen et al. (2006) observed a reduction of the N170 amplitude for 'thatcherized' faces compared to natural faces. The N170 was also observed to be of larger amplitude for asymmetrical than symmetrical faces and for top-heavy faces than for bottom-heavy faces (Macchi Cassia et al., 2006). With regard to second-order configuration, Halit et al. (2000) observed that elongation of faces did not influence the N170, whereas this component was larger for faces judged as atypical than for faces judged as typical. Moreover, Scott and Nelson (2006) observed that lateralization of the N170 component was influenced by featural and second-order configural differences in faces, although they found that the general amplitude of the N170 was not influenced by these differences in faces. When a difference waveform was calculated by subtracting the N170 response to the manipulated face from that of the familiarized face, the amplitude of this difference was significantly larger in the left hemisphere for featural than for configural manipulations, whereas the opposite was observed in the right hemisphere. Thus, the available literature suggests that the N170 ERP component could be sensitive to the first-order configuration of a face, as well as to some aspects of its second-order configuration and to the eye features, which is congruent with the idea that this component reflects the structural encoding stage of face processing.

The P2 component has a similar topography as the P1 component (Curran et al., 1993; Tucker et al., 1994), and may reflect the re-activation of the primary and secondary visual areas in a process of visual cortical feedback (Kotsoni et al., 2006, 2007). The literature reveals modulations of the P2 component by modifications of the first-order configuration ('thatcherization'; Boutsen et al., 2006) and second-order configuration (elongation; Halit et al., 2000) of a face, but it is not clear if this component is also sensitive to featural processing of faces.

The first aim of this experiment was to explore the brain processes involved in the discrimination of individual faces by systematically investigating the influence of feature and second-order configuration modifications of face stimuli on ERP components. In the first part of the experiment, participants were asked to judge whether pairs of faces that sometimes differed on their features or second-order configuration were the same or different. This task does not explicitly direct attention to either aspect of face processing, although the modifications of the face stimuli may implicitly direct attention to the features or configuration of these stimuli. The second aim of this experiment was to determine whether explicitly instructing participants to attend to the features or to the configuration of faces would influence the neural processes involved for these stimuli. By varying the experimental task to direct attention to the *features* of a face, it was expected that the whole face would be processed with a more local strategy, whereas directing attention to the *configuration* of a face would elicit a global processing strategy. In analogy with the influence of local/global processing strategies on the neural processes involved for hierarchical stimuli[1] (Martínez et al., 1997; Moses et al., 2002), we hypothesized that some face-sensitive ERP components would be modified by tasks aimed at shifting attentional focus to features or configuration. To test this hypothesis, the second part of the experiment presented pairs of faces that always differed in their features *or* in their second-order configuration. Participants were asked to attend to the features *or* to the configuration in these faces and to decide if there was a difference in the attended aspect while ignoring other differences. This task is similar to the one used with hierarchical stimuli by Moses et al. (2002) and Martínez et al. (1997), where participants were asked to attend to either the local or global level of hierarchical stimuli and decide if a target shape or letter was present at the attended level. The stimuli used for this experiment were the "Jane stimuli" (Mondloch et al., 2002). We analyzed the impact of these tasks and stimulus conditions on the amplitude of the P1, N170 and P2 components. The P300 component was also studied to find

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[1] A large form at the global level (for example the letter A) composed of many smaller forms at the local level (for example letters B).

if the two tasks were successful in varying the processing strategies. Since this component is generally larger for target stimuli (Luck, 2005), we predicted that the P300 would be larger for faces with a feature modification in the featural task and larger for faces with a configuration modification in the configural task if the tasks successfully influenced the participant's focus of attention.

2. Results

2.1. *Behavioral results*

A one-way ANOVA revealed that the accuracy was influenced by the task. Participants were more accurate in the featural task than in the same–different task or the configural task (see Fig. 1 and Table 1). A one-way ANOVA in the same–different task revealed that the accuracy differed across stimulus category, with more errors to Configuration and Original stimuli than to Feature stimuli. In the featural task there was no significant difference between the two types of stimuli, whereas in the configural task there were more errors on the Configuration stimuli than on the Feature stimuli. Response times were also influenced by the task, with faster responses in the featural task than in either the configural or same–different task. In the same–different task, the stimulus type also influenced response times, with faster responses to Feature stimuli than to Configuration and Original stimuli. Feature stimuli were also associated with faster response times compared to Configuration stimuli in both the featural task and the configural task.

Table 1 – Results of statistical tests on behavioral data

	Error rate	Response times
Influence of task	$F(2, 11)=11.0$; $p=0.002$ Posthoc *t*-tests Same–different vs. Featural: $t(12)=4.0$; $p=0.002$ Same–different vs. Configural: $t(12)=-1.6$; $p=0.129$ Featural vs. Configural: $t(12)=-3.0$; $p=0.012$	$F(2, 11)=4.8$; $p=0.031$ Posthoc *t*-tests Same–different vs. Featural: $t(12)=2.1$; $p=0.053$ Same–different vs. Configural $t(12)=-3.6$; $p=0.728$ Featural vs. Configural: $t(12)=-2.6$; $p=0.024$
Influence of different task stimulus in the same–different task	$F(2, 11)=26.1$; $p<0.001$ Posthoc *t*-tests Original vs. Feature: $t(12)=4.0$; $p=0.002$ Original vs. Configuration: $t(12)=-0.7$; $p=0.494$ Feature vs. Configuration: $t(12)=-3.9$; $p=0.002^*$	$F(2, 11)=17.1$; $p<0.001$ Posthoc *t*-tests Original vs. Feature: $t(12)=3.4$; $p=0.005$ Original vs. Configuration: $t(12)=0.6$; $p=0.572$ Feature vs. Configuration: $t(12)=-3.3$; $p=0.006$
Influence of stimulus in the featural task	$t(12)=0.8$; $p=0.416$	$t(12)=2.5$; $p=0.027$
Influence of stimulus in the configural task	$t(12)=2.7$; $p=0.018$	$t(12)=3.3$; $p=0.006$

F or *t*(*df*); *p*.

2.2. *ERP results*

ERP correlates for the second face of each pair were of most interest and were analyzed in two separate ANOVAs for each ERP component. The first ANOVA targeted Part 1 and was a Stimulus (Original, Feature, Configuration) × Hemisphere (Left, Right) repeated measures ANOVA (results of this ANOVA for each ERP component are presented in Table 2), followed by posthoc *t*-tests on individual contrasts. It aimed to analyze how the ERPs were influenced by feature and configuration manipulations in a simple same–different task. The second ANOVA targeted Part 2 and was a Task (Featural,

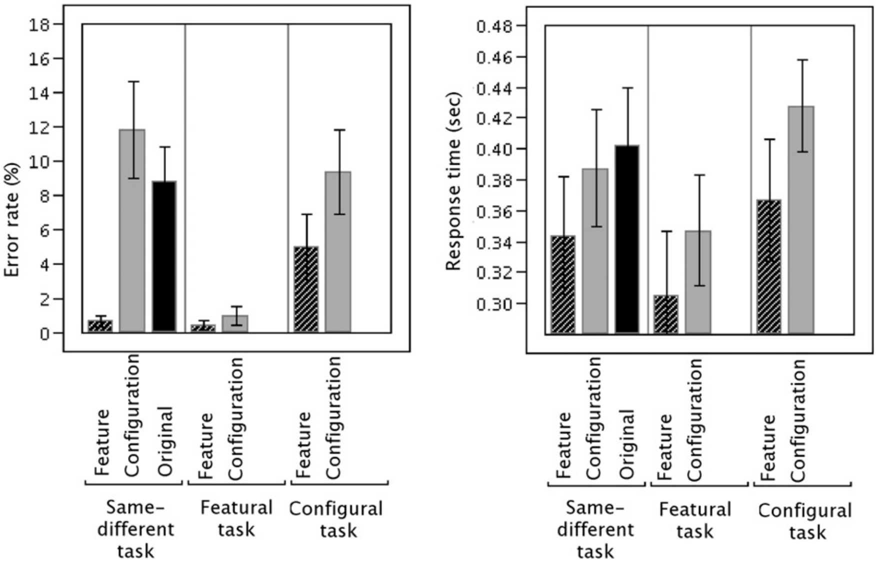

Fig. 1 – Mean error rates and response times in each condition.

Table 2 – Results of ANOVAs on each ERP components in Parts 1 and 2

	P1	N170	P2	P300
Part 1: Stimulus × Hemisphere ANOVA				
Stimulus	(2, 11) = 4.2; 0.043	(2, 11) = 1.5; 0.261	(2, 11) = 7.3; 0.010	(2, 11) = 68.3; < 0.001
Hemisphere	(1, 12) = 0.2; 0.659	(1, 12) = 0.4; 0.521	(1, 12) = 0.2; 0.694	(1, 12) < 0.1; 0.851
Stimulus × Hemisphere	(2, 11) = 0.5; 0.638	(2, 11) = 0.1; 0.914	(2, 11) = 0.8; 0.464	(2, 11) = 6.7; 0.013
Part 2: Stimulus × Task × Hemisphere ANOVA				
Stimulus	(1, 12) = 0.5; 0.475	(1, 12) = 2.0; 0.182	(1, 12) = 13.0; 0.004	(1, 12) = 0.2; 0.693
Task	(1, 12) = 1.4; 0.266	(1, 12) = 1.0; 0.343	(1, 12) = 1.4; 0.266	(1, 12) = 1.8; 0.205
Hemisphere	(1, 12) = 0.1; 0.760	(1, 12) < 0.1; 0.842	(1, 12) = 0.3; 0.624	(1, 12) < 0.1; 0.841
Stimulus × Task	(1, 12) = 0.2; 0.675	(1, 12) = 0.2; 0.687	(1, 12) = 0.2; 0.659	(1, 12) = 8.4; 0.013
Stimulus × Hemisphere	(1, 12) = 0.9; 0.370	(1, 12) = 0.2; 0.669	(1, 12) = 0.3; 0.579	(1, 12) < 0.1; 0.935
Task × Hemisphere	(1, 12) = 0.4; 0.518	(1, 12) < 0.1; 0.865	(1, 12) = 0.2; 0.626	(1, 12) = 1.5; 0.246
Stimulus × Task × Hemisphere	(1, 12) = 0.4; 0.536	(1, 12) = 0.3; 0.585	(1, 12) < 0.1; 0.994	(1, 12) = 10.0; 0.008

F(df); p.

Configural) × Stimulus (Feature, Configuration) × Hemisphere (Left, Right) repeated measures ANOVA (results of this ANOVA for each ERP component are presented in Table 2), followed by posthoc *t*-tests on individual contrasts. The aim of this ANOVA was to analyze how the ERPs were modulated by the different tasks. Fig. 2 illustrates the morphology of the grand-average waveform in each condition. Effects that had $p<0.05$ were considered as significant and *p*-values were not corrected for multiple comparisons.

2.3. P1

In Part 1 the stimulus had a significant influence on the P1 peak amplitude, with a larger P1 for Feature stimuli compared to Configuration stimuli [$t(12)=3.0$; $p=0.011$]. The P1 elicited by the original face did not differ from that of the modified faces [Feature vs. Original; $t(12)=1.1$; $p=0.305$; Configuration vs. Original: $t(12)>-0.1$; $p=0.976$]. In Part 2 no factor or interaction was significant.

2.4. N170

In Part 1 no factor or interaction influenced the peak amplitude of the N170, suggesting that this component was not influenced by feature and second-order configuration manipulations. In Part 2 no factor or interaction influenced the peak amplitude of the N170, suggesting that the featural vs. configural task did not modulate the N170.

2.5. N170 difference waveform

Because Scott and Nelson (2006) found a difference in lateralization of the N170 when computing a difference-wave between the altered face and the familiarized face, a difference-wave was computed for the configural task, between the Configuration stimulus and the Original stimulus, and for the featural task between the Feature stimulus and the Original stimulus. The amplitude was extracted in the same time-window as used for the N170. However, no effect of Hemisphere [$F(1, 12)=0.1$; $p=0.745$] or Task [$F(1, 12)=0.5$; $p=0.502$] was observed, and there was no interaction between these two factors [$F(1, 12)=0.3$; $p=0.570$].

2.6. P2

In Part 1 only Stimulus had a significant effect on the peak amplitude of the P2 component. Posthoc *t*-tests revealed that Feature stimuli elicited a smaller P2 than did Configuration [$t(12)=-4.0$; $p=0.002$] and Original stimuli [$t(12)=-2.7$; $p=0.017$]. In Part 2 Stimulus also had a similar effect, with a smaller P2 amplitude for Feature stimuli than for Configuration stimuli.

2.7. P300

In Part 1 a significant effect of Stimulus was observed on the amplitude of the P300, where Feature > Configuration > Original [Feature vs. Configuration: $t(25)=5.2$; $p<0.001$; Feature vs. Original: $t(25)=13.0$; $p<0.001$; Configuration vs. Original: $t(25)=9.5$; $p<0.001$]. There was also a significant interaction between Hemisphere and Stimulus, which was driven by a larger Feature > Configuration difference in the right hemisphere [$t(12)=4.5$; $p<0.001$] than in the left hemisphere [$t(12)=3.0$; $p=0.012$]. In Part 2 there was a significant interaction between Stimulus and Task. In the featural task, Feature stimuli elicited a larger P300 than Configuration stimuli [$t(25)=2.5$; $p<0.020$], whereas the opposite was true in the configural task [$t(25)=-2.8$; $p=0.010$]. In other words, the P300 was larger when the faces presented a difference in the attended aspect (feature or configuration), than when the difference was observed in the non-attended aspect. There was also a significant 3-way interaction between Stimulus, Task and Hemisphere. Separate ANOVAs by Hemisphere revealed that the Stimulus × Task interaction was significant in the left [$F(1, 12)=13.2$; $p=0.003$], but not in the right hemisphere [$F(1, 12)=2.0$; $p=0.180$], suggesting that the previously described pattern arose mainly from the left hemisphere.

3. Discussion

This experiment studied the ERP correlates of featural and configural face processing. Part 1 explored how features and second-order configuration modifications in faces affect early ERP components. Part 2 tested the hypothesis that ERP correlates of faces could be modulated by instructing

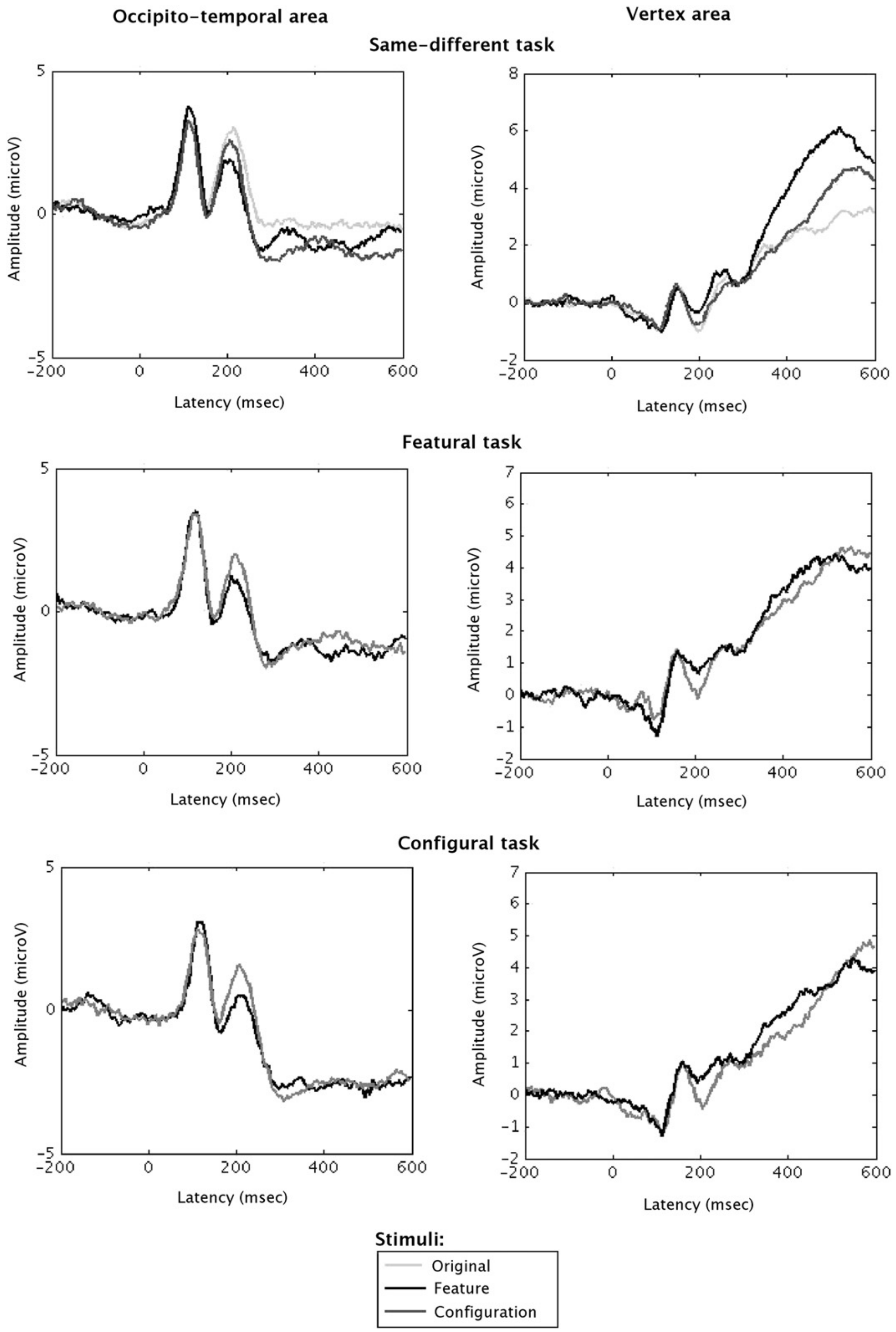

Fig. 2 – Grand-average waveform in the occipito-temporal and vertex areas.

participants to attend to the features or the configuration of face stimuli.

The behavioral results from this study were congruent with previous results using the same (LeGrand et al., 2006; Maurer et al., 2007; Mondloch et al., 2002) or similar stimuli (Freire et al., 2000). Indeed, it was observed that adults were more accurate in a same–different task when faces had a difference in features rather than a difference in configuration. The present study extended these results by showing that participants were also faster and more accurate when asked to judge similarity of face features rather than face configuration. Specifically, participants had a tendency to overlook differences in the configuration, as revealed by a larger error rate in the configural task on the Configuration stimuli (misses) than on the Feature stimuli (false alarms).

3.1. *Influence of feature and second-order configuration differences in faces*

The first part of the experiment explored how subtle differences in the features or configuration of faces were encoded in the brain without prior instruction. The literature suggested that ERP components as early as the P1 could be sensitive to these dimensions of face processing. The results of the present study suggested that the P1 component was influenced by manipulations of face stimuli in the same–different task. Indeed, it was observed that the P1 was larger for Feature stimuli than for Configuration stimuli. This result is congruent with the fMRI findings of Maurer et al. (2007). Using the same stimuli as in the present study, they observed that faces with featural modifications elicited more activation in posterior areas of the visual cortex than faces with configural modifications, a result that they attributed to the greater low-level stimulus changes in the featural stimuli. It is possible that the P1 effect observed in the present experiment and the difference in the BOLD response of the early visual cortex reflect the same neural activity. However, there were no significant difference observed between the modified categories and the original stimulus, and this Feature>Configuration difference was not replicated in the following two tasks. Overall, these results do not support the idea that the P1 is reliably influenced by modifications of the features or second-order configuration.

The results of the present experiment showed no modulation of the N170 by modifications of features or second-order configuration in faces. Previous studies have found that the P1 and N170 can be influenced by some configuration manipulations, for example 'thatcherization' (Boutsen et al., 2006), vertical symmetry and up–down featural arrangement (Macchi Cassia et al., 2006). Halit et al. (2000) also found that faces judged as atypical elicited a larger P1 and N170 than faces judged more typical, but that elongating a face influenced P1 and not N170. One possibility is that the manipulations presented in the current experiment were too close to the prototypical face to influence the amplitude of the P1 or N170. These components would be more influenced by manipulations that violate the natural first-order configuration of a face (such as those presented by Boutsen et al. and by Macchi Cassia et al.), than by subtle manipulations of features or second-order configuration.

The discrepancy between the present results and those of Scott and Nelson (2006) can possibly be explained by a difference in the construction of the stimuli. As in the present study, these authors found no influence of feature and second-order configuration manipulations on the N170 itself. However, they found a lateralized influence of these manipulations on the difference-wave between the manipulated and the familiarized face, which was not observed in the present study in the difference-wave between the modified faces and the original face. The Jane stimuli were created to remain within the natural variation of human faces, which resulted in configuration differences being more difficult to recognize than feature differences. As stated earlier, Configuration stimuli were associated with a lower accuracy and longer response times than Feature stimuli. Scott and Nelson (2006) did not have this discrepancy between their two stimulus categories because their stimuli were matched for difficulty level at creation. As a consequence, the spacing manipulations were larger than the ones that created the Jane stimuli, probably going beyond the natural variation of human faces. As a consequence, the modulation of the N170 in that study may reflect the recognition of an unnatural face configuration.

In an fMRI study with the same stimuli, Maurer et al. (2007) observed lateralized differences in the cortical areas involved in featural and configural face processing. The areas that showed greater activity for featural processing of faces were mostly located in the left prefrontal areas, whereas areas of the right fusiform gyrus and of the right frontal cortex showed more activity in configural face processing. This lateralization pattern is congruent with the asymmetries generally observed for local/global processing of hierarchical stimuli (Martínez et al., 1997; Moses et al., 2002). In the present study, the only significant effects of hemisphere were found on the P300 component, but these asymmetries were not congruent with the local/global asymmetries. Indeed, in Part 1, the Feature>Configuration difference was larger in the right than in the left hemisphere, which is inconsistent with a superiority of the right hemisphere for configural processing. In Part 2, the statistical interaction between the stimulus and the task was stronger in the left than in the right hemisphere. Taken together, these results suggest that the left P300 could be more reliable in dissociating targets and non-targets than the right P300. In Part 2, this is revealed by a larger P300 amplitude in the left hemisphere for stimuli with a task-relevant modification than for stimuli with an irrelevant modification. In Part 1, features and configuration modifications were equally task-relevant and the left P300 showed less difference between these two categories than the right P300. In other words, these results suggest that there might be hemispheric differences in the target detection processes that cannot be attributed to asymmetries in local/global processes. No ERP component showed this local/global pattern of lateralization, suggesting that the neural activity giving rise to these hemispheric asymmetries could occur at later latencies after the stimulus presentation.

As opposed to earlier components, the P2 component in this study was modulated by the type of manipulations presented in face stimuli. This component was reduced in amplitude when elicited by faces with a feature manipulation than when elicited by faces with a configuration manipulation or the original face. This effect was independent of the task in which the stimuli were presented. Previous studies have suggested that the P2 component may reflect the effects of visual cortical feedback (Kotsoni et al., 2006, 2007). In the present experiment, feature differences were more salient than configuration differences, as revealed by faster response times and higher accuracy. Therefore, stimuli with a configuration manipulation, or stimuli with no manipulation, may require more thorough visual analysis (and possibly enhanced cyclical activity in the feedback loop) in order to perform a same or different task. This may explain the longer response time, the lower accuracy and the larger P2. This P2 activity was not influenced by tasks aiming to modulate processing strategies. In light of these findings, it is suggested that the P2 observed in this study may reflect the cortical activity associated with searching for differences in these pairs of faces, whereas the activity associated with deciding which of these differences were task-specific was observed later, at the level of the P300. We suggest that the P2 component in this study may reflect visual feedback activity in terms of depth of processing, but not in terms of strategic factors. Further research is required to determine if this effect is specific to faces or if it generalizes to other stimuli with a local and global organization. Previous results also suggest that 'thatcherized' faces presented in a chair or house detection task (Boutsen et al., 2006) and elongated faces presented in passive viewing (Halit et al., 2000) elicit a reduced amplitude P2 compared to normal faces. It is possible that higher visual areas elicit more activity in the cortical feedback loop when a stimulus has a configuration for which the participant is expert, than when the stimulus differs from this over-practiced configuration (for example if 'thatcherized' or elongated). This increased depth of processing for objects of expertise could reflect the extraction of multiple levels of information (including configural information) necessary for the discrimination of these stimuli at the individual level. This hypothesis is congruent with the results of Stahl et al. (2008) who observed a P2 of larger amplitude for own-race faces (Caucasian) than for other-race faces (Asian), only in participants without considerable experience regarding Asian people. The authors attributed this result to the fact that holistic processing plays a more important role in the processing of own-race than other-race faces (Tanaka et al., 2004). Based on this hypothesis, we would predict that the P2 component would increase in amplitude when a participant develops a visual expertise such as learning to discriminate individuals of a new object category (for example greebles) or learning to read. Also, it has been previously observed that configural face processing develops more slowly than featural face processing (Mondloch et al., 2002, 2006). Therefore, it is possible that the amplitude of the P2 ERP component develops with the development of this additional aspect of face processing. In this respect, it would be expected to find a larger P2 in children with better configural face processing skills.

3.2. *Influence of featural and configural processing strategies*

The second part of the present experiment studied how ERP components are modulated when a participant attends to the features or the configuration in a face. The pattern of modulations of the P300 component in the present study suggests that the tasks were successful in varying the attentional focus on these aspects of face processing. Indeed, the P300 was enhanced when a participant observed a difference in the attended aspect of a face compared to other differences. In Part 1, the P300 was larger to Feature and Configuration stimuli than to the original face. In Part 2, the P300 was larger for the Configuration stimuli in the configural task and the Feature stimuli in the featural task. This pattern is consistent with the proposal that the P300 component is enhanced for target stimuli (Luck, 2005) and confirms that these two tasks successfully varied the participant's focus of attention. The fact that the P300 was larger for Feature stimuli than for Configuration stimuli in Part 1 is also consistent with the notion that the P300 is smaller when a participant is uncertain of whether a stimulus is a target or a non-target (Luck, 2005). Indeed, the behavioral data and the comments given by participants strongly suggest that there were more uncertainties in the responses to Configuration stimuli than to Feature stimuli in Part 1.

However, no influence of processing strategies was observed on other ERP components. This suggests that featural/configural processing strategies might not influence the early cognitive processes reflected by these ERP components, but that they could potentially influence the pattern of brain activity at later latencies. Moreover, given the low spatial resolution of the ERP technique, it would be interesting to use fMRI to find if differences in lateralization would be observed when participants attend to the features or the configuration of faces in the specific areas of the occipito-temporal region also involved in local/global processing of hierarchical stimuli (Martínez et al., 1997; Moses et al., 2002).

To conclude, this study revealed that the P2 component was reliably influenced by subtle differences in the features and second-order configuration of face stimuli. Although this P2 activity was not influenced by experimental tasks aiming to modify processing strategies, this result suggests that the processing of the configural aspect of a face could require a more in-depth visual analysis (and possibly more cortical visual feedback) than the processing of its features. On the other hand, varying the focus of attention on the features or configuration of a face influenced the P300 component, which suggests that this component could be involved in the cognitive process of identifying which of the facial differences were task-relevant. Finally, this study did not reveal modulations of the P1 and N170 by features and second-order configuration differences in faces, suggesting that these components could be more sensitive to differences that affect the natural first-order configuration of a face.

4. Experimental procedures

4.1. *Participants*

13 participants between 22 and 38 years old (mean age=28; 9 females) were paid for their participation. These participants were right-handed according to a modification of the Edinburgh Handedness Inventory and had normal or corrected-to-normal vision. They reported no language, reading or learning disorders, and none reported taking any psychoactive drug. The experiment was undertaken with the understanding and written consent of each participant.

4.2. *Stimuli*

The stimuli used for this experiment were the "Jane stimuli" (Mondloch et al., 2002). These are grey-scale images of Caucasian female faces with a surgical cap covering their hair and ears to discourage the use of non-face features in their discrimination. All pictures were derived from the same original face, named ‘Jane’. Mondloch et al. manipulated this original face to create the ‘Jane's sisters’ stimuli (see Fig. 3). In the present experiment, two stimulus sets were used: the features modifications set and the configuration modifications set, with four faces per set. Faces with featural modifications were created by replacing the original eyes and mouth with the eyes and mouth of another female face. Faces with spacing (or configuration) differences were created by moving the eyes up or down relative to the original, closer together or farther apart, or by moving the mouth up or down (see Mondloch et al., 2002, for more details on stimulus construction). Spacing modifications were used as second-order configuration manipulations since they represent natural variations in faces and hence involve ‘normal’ face processing. The pictures were 10.2×15.2 cm or 288×432 pixels, and subtended 7.3×10.9° of visual angle from a distance of 80 cm.

4.3. *Procedure*

EEG signal was recorded using a Geodesic Sensor Net with 128 electrodes (Tucker, 1993), with vertex as reference; horizontal and vertical electro-oculograms were used to monitor eye movements. EGI NetAmps 200 was used (gain = 1000), data were digitized with sampling rate of 250 Hz, and band-pass filtered between 0.1 and 100 Hz. The experiment was presented in three parts. In Part 1 (same–different task), pairs of faces were presented, with the first item of the pair always being the original face, followed either by the original face again (in 50% of trials), a face with a feature manipulation (25% of trials), or a face with a configuration manipulation (25% of trials). The participant's task was to judge if the two items of the pair represented the same face or different faces. Responses were given by pressing one of two buttons on a joystick, where a response with the right index finger indicated ‘same’ and a response with the left index finger indicated ‘different’. Part 1 began with the presentation of a practice phase composed of 16 trials (8 pairs in which the faces were identical, 4 pairs in which the faces differed in their features and 4 pairs in which the faces differed in their configuration), which was repeated if the participant made more than two errors. The experimental phase comprised two blocks of 112 trials each. After completion of Part 1, the participant was shown the original and modified faces, and his/her attention was drawn to the fact that some of these images had feature manipulations and some had configuration manipulations. The participant was then informed that, in the rest of the experiment, he/she would be instructed to focus on one or the other type of modifications only. In Part 2, pairs of stimuli were presented, with the first item of the pair being the original face and the second item being a face with a feature manipulation (50%) or a configuration manipulation (50%). In the featural task, the participant had to judge if the *features* in the two items of the pair were the same or different; in the configural task, the participant had to judge if the *configuration* of the two faces was the same or different. In each of these parts a practice phase of eight items (4 pairs in which the faces differed in their features and 4 pairs in which the faces differed in their configuration) was presented and was repeated until the participant was able to complete all eight items making only two errors or less. The experimental phase consisted of two blocks of 64 trials in each task for Part 2, with block order counterbalanced. Each trial began with the presentation of a central fixation point for 500 ms. The original face was then presented in the middle

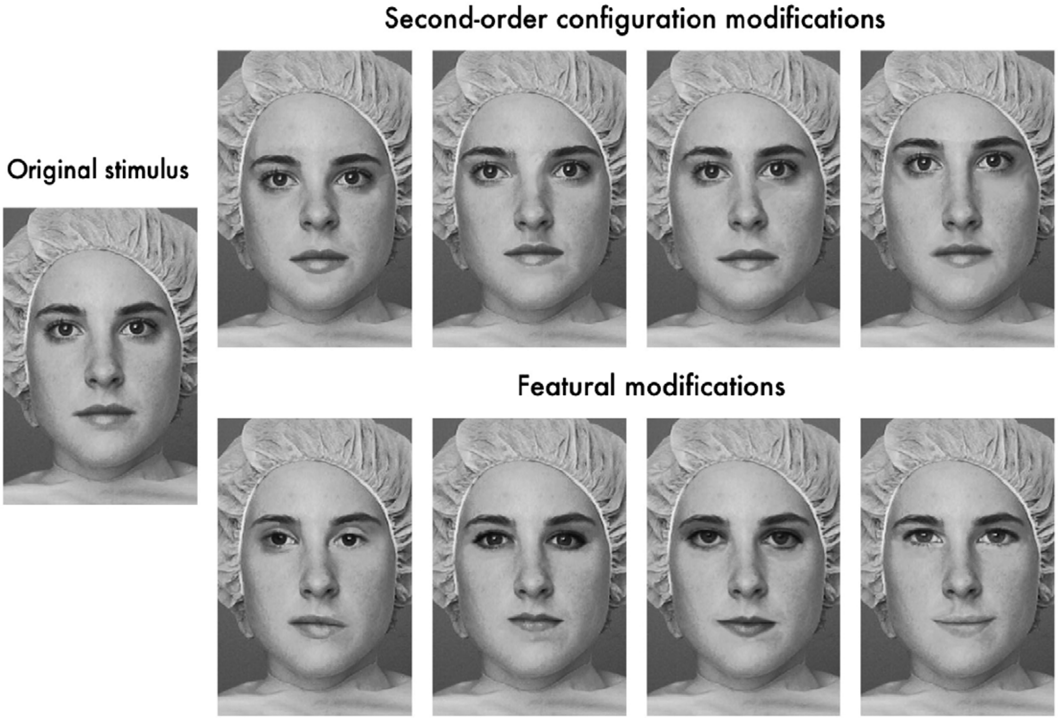

Fig. 3 – The Jane stimuli.

of the screen for 700 ms, followed by a fixation cross for a random duration ranging from 200 to 400 ms. The second picture of the pair was then presented for 700 ms, followed by a question mark lasting between 1200 and 1400 ms. The participant was instructed not to respond until the appearance of this question mark. The stimuli were displayed on a 21-inch monitor using Matlab on a Mac OSX computer.

4.4. *ERP waveform analysis*

Each trial was segmented from the continuous EEG data (windowed from 200 ms pre-stimulus onset to 600 ms post-stimulus onset). Segments were individually inspected for artifacts; signal from rejected electrodes was replaced using the 'bad channel replacement' algorithm in Nestation 4.2. If more than 10 of 128 channels were rejected, the trial was not included in the average. No participant had more than one third of the trials rejected in any category. Waveforms were baseline-corrected using the 200 ms pre-stimulus interval. Averages were computed for each participant in each experimental condition, and data re-referenced to the average of channels. Based on visual inspection of the grand average, a montage of electrodes was created where the P1, N170 and P2 components were maximal in the right and left occipito-temporal regions (left: 57, 58, 59, 60, 63, 64, 65, 66, 67, 69, 70, 71, 72, 74, 75; right: 77, 78, 83, 84, 85, 86, 89, 90, 91, 92, 95, 96, 97, 100, 101). Because the P300 was maximal around the vertex, different montages were created for this component (vertex left= 7, 13, 31, 32, 37, 38, 43, 53, 54, 61; vertex right= 79, 80, 81, 87, 88, 94, 105, 106, 107, 113). Based on visual inspection of the individual data, the time-windows were defined as follows: P1 (67–151 ms), N170 (111–187 ms), P2 (163–239 ms), P300 (347–699 ms). The component peak amplitude within this time-window was extracted for each participant, in each condition, for the average of all channels in the left and in the right hemisphere montages.

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REFERENCES

Bentin, S., Deouell, L.Y., 2000. Structural encoding and identification in face processing: ERP evidence for separate mechanisms. Cogn. Neuropsychol. 17 (1/2/3), 35–54.

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. Cogn. Neuropsychol. 8 (6), 551–565.

Bentin, S., Sagiv, N., Mecklinger, A., Friederici, A., von Cramon, Y.D., 2002. Priming visual face-processing mechanisms: electrophysiological evidence. Psychol. Sci. 13 (2), 190–193.

Boutsen, L., Humphreys, G.W., Praamstra, P., Warbrick, T., 2006. Comparing neural correlates of configural processing in faces and objects: an ERP study of the Thatcher illusion. NeuroImage 32, 352–367.

Curran, T., Tucker, D.M., Kutas, M., Posner, M.I., 1993. Topography of the N400: brain electrical activity reflecting semantic expectancy. Electroencephalogr. Neurophysiol. 88, 188–209.

Eimer, M., 2000. Event-related brain potentials distinguish processing stages involved in face perception and recognition. Clin. Neurophysiol. 111 (4), 694–705.

Freire, A., Lee, K., Symons, L.A., 2000. The face-inversion effect as a deficit in the encoding of configural information: direct evidence. Perception 29, 159–170.

Halit, H., de Haan, M., Johnson, M.H., 2000. Modulation of event-related potentials by prototypical and atypical faces. NeuroReport 11 (9), 1871–1875.

Kotsoni, E., Mareschal, D., Csibra, G., Johnson, M.H., 2006. Common-onset visual masking in infancy: behavioral and electrophysiological evidence. J. Cogn. Neurosci. 18 (6), 1–8.

Kotsoni, E., Csibra, G., Mareschal, D., Johnson, M.H., 2007. Electrophysiological correlates of common-onset visual masking. Neuropsychologia 45 (10), 2285–2293.

LeGrand, R., Cooper, P.A., Mondloch, C.J., Lewis, T.L., Sagiv, N., de Gelder, B., et al., 2006. What aspects of face processing are impaired in developmental prosopagnosia? Brain Cogn. 61, 139–158.

Luck, S.J., 2005. An Introduction to the Event-related Potential Technique. The MIT Press, Cambridge, Massachussets.

Macchi Cassia, V., Kuefner, D., Westerlund, A., Nelson, C.A., 2006. Modulation of face-sensitive event-related potentials by canonical and distorted human faces: the role of vertical symmetry and up–down featural arrangement. J. Cogn. Neurosci. 18 (8), 1343–1358.

Martínez, A., Moses, C.P., Frank, L., Buxton, R., Wong, E., Stiles, J., 1997. Hemispheric asymmetries in global and local processing: evidence from fMRI. NeuroReport 8 (7), 1685–1689.

Maurer, D., Le Grand, R., Mondloch, C.J., 2002. The many faces of configural processing. Trends Cogn. Sci. 6 (6), 255–260.

Maurer, D., O'Craven, K.M., Le Grand, R., Mondloch, C.J., Springer, M.V., Lewis, T.L., et al., 2007. Neural correlates of processing facial identity based on features versus their spacing. Neuropsychologia 45, 1438–1451.

Mondloch, C.J., Le Grand, R., Maurer, D., 2002. Configural face processing develops more slowly than featural face processing. Perception 31 (5), 553–566.

Mondloch, C.J., Leis, A., Maurer, D., 2006. Recognizing the face of Johnny, Suzy, and Me: insensitivity to the spacing among features at 4 years of age. Child Dev. 77 (1), 234–243.

Moses, P., Roe, K., Buxton, R.B., Wong, E.C., Frank, L.R., Stiles, J., 2002. Functional MRI of global and local processing in children. NeuroImage 16, 415–424.

Schyns, P.G., Jentzsch, I., Johnson, M.H., Schweinberger, S.R., Gosselin, F., 2003. A principled method for determining the functionality of brain responses. NeuroReport 14 (13), 1665–1669.

Scott, L.S., Nelson, C.A., 2006. Featural and configural face processing in adults and infants: a behavioral and electrophysiological investigation. Perception 35, 1107–1128.

Stahl, J., Wiese, H., Schweinberger, S.R., 2008. Expertise and own-race bias in face processing: an event-related potential study. NeuroReport 19 (5), 583–587.

Tanaka, J.W., Kiefer, M., Bukach, C.M., 2004. A holistic account of the own-race effect in face recognition: evidence from a cross-cultural study. Cognition 93, B1–B9.

Tucker, D.M., 1993. Spatial sampling of head electrical fields: the geodesic sensor net. Electroencephalography and Clinical Neurophysiology 87, 154–163.

Tucker, D.M., Liotti, M., Potts, G.F., Russell, G.S., Posner, M.I., 1994. Spatiotemporal analysis of brain electrical fields. Hum. Brain Mapp. 1, 134–152.