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Asymmetric switch-costs and ERPs reveal facial identity dominance over expression

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ABSTRACT

Previous studies on face processing have revealed an asymmetric overlap between identity and expression, as identity is processed irrespective of expression while expression processing partly depends on identity. To investigate whether this relative interaction is caused by dominance of identity over expression, participants performed familiarity and expression judgments during task switching. This paradigm reveals task-set dominance with a paradoxical asymmetric switch-cost (i.e., greater difference between switch and repeat trials when switching toward the dominant task). Event-related potentials (ERPs) were recorded to find the neural signature of the asymmetric cost. As expected, greater switch-cost was shown in the familiarity task with respect to response times, indicating its dominance over the expression task. Moreover, a left-sided ERP correlate of this effect was observed at the level of the frontal N2 component, interpreted as an index of modulations in endogenous executive control. Altogether, these results confirm the overlap between identity and expression during face processing and further indicate their relative dominance.

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1. Introduction

Faces are one of the most salient stimuli for humans, as they convey information about identity, emotion, gender, age, social status, and so on. One intriguing question investigated for the last thirty years concerns interactions between facial dimensions, especially identity and emotional expression. In the traditional view of face processing, identity and expression involve independent and parallel visual systems (Bruce & Young, 1986), an assumption supported by neuropsychological (Tranel, Damasio, & Damasio, 1988), and behavioral (Campbell, Brooks, de Haan, & Roberts, 1996; Young, McWeeny, Hay, & Ellis, 1986) studies as well as neuroimaging (Sergent, MacDonald, & Zuck, 1994), and event-related potentials (ERP) (Bobes, Martin, Olivares, & Valdés-Sosa, 2000; Caharel, Courtay, Bernard, Lalonde, & Rebaï, 2005) recordings. However, several studies in the last decade indicate overlapping between the two dimensions in neurologic and psychiatric patients (Baudouin, Martin, Tiberghien, Verlut, & Franck, 2002; Gallegos & Tranel, 2005; Martin, Baudouin, Tiberghien, & Franck, 2005), as well as in healthy subjects (Bate, Haslam, & Hodgson, 2009; Baudouin, Gilibert, Sansone, & Tiberghien, 2000; Campbell & Burke, 2009; Dobel et al., 2008; Ellamil, Susskind, & Anderson, 2008; Fox, Oruç, & Barton, 2008, 2009; Fox, Young Moon, Iaria, & Barton, 2009; Ganel & Goshen-Gottstein, 2004; Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Kaufmann & Schweinberger, 2004; Lander & Metcalfe, 2007; Leleu et al., 2010; Schweinberger & Soukup, 1998; Schweinberger, Burton, & Kelly, 1999; Vuilleumier, Armony, Driver, & Dolan, 2001; Wild-Wall, Dimigen, & Sommer, 2008). Relative interactions between the two processes are also proposed in a recent model of face perception based on principal component analysis (Calder & Young, 2005).

1.1. The nature of interactions between facial identity and expression

The term "relative" indicates different degrees of dependencies between identity and expression. The first probing illustration of a relative interaction between the two face dimensions was found by the seminal work of Schweinberger and Soukup (1998). Using the selective attention paradigm described by Garner (1976), they showed that subjects are able to attend selectively to identity regardless of the emotion expressed, whereas expression classifications are strongly influenced by irrelevant information on identity. Other studies have found the same kind of interaction with the Garner-type paradigm in healthy participants (Schweinberger et al., 1999) and schizophrenic patients (Baudouin et al., 2002; Martin et al., 2005). More recently, data on visual aftereffects show adaptation to expression partly depending on features important for identity, while representations of identity are independent of variations in expression (Campbell & Burke, 2009; Ellamil et al., 2008; Fox et al., 2008). In addition, fMRI

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studies provide evidence of functional overlap in the cortical network of face processing proposed by Haxby, Hoffman, and Gobbini (2000). Although the fusiform face area (FFA) and the superior temporal sulcus (STS) are associated respectively with identity and expression processing in the core system of this model, greater activation can be observed in the FFA when subjects attend to either identity or expression and in the STS when they only attend to expression (Fox et al., 2009; Ganel et al., 2005; Vuilleumier et al., 2001).

There are cases where expression influences identity processing, especially for familiar faces. Using the Garner-type paradigm, Ganel and Goshen-Gottstein (2004) observed greater interference for familiar than for unknown faces in both identity and expression judgments. Furthermore, there is a body of research that supports the idea of more accurate and/or faster recognition of familiar faces expressing happiness (Bate et al., 2009; Baudouin et al., 2000; Dobel et al., 2008; Gallegos & Tranel, 2005; Kaufmann & Schweinberger, 2004; Lander & Metcalfe, 2007; Wild-Wall et al., 2008), whereas some studies found reduced familiarity judgments for negativeexpression faces (Bate et al., 2009; Dobel et al., 2008; Lander & Metcalfe, 2007; Leleu et al., 2010). These interactions may gradually appear as soon as learned faces become familiar and are stored in memory, probably due to their affective value. On the contrary, expression processing is always influenced by the identity of the face irrespective of its familiarity, suggesting that the expression analysis system necessarily takes into account individual identity due to an adaptive bias (e.g., Schweinberger & Soukup, 1998). The most compelling interpretation of all findings with familiar and unknown faces is that systems processing identity and expression are partially interconnected, in that facial identity serves as a reference from which expressions are more easily but not exclusively derived (Ellamil et al., 2008; Fox et al., 2008, 2009; Ganel & Goshen-Gottstein, 2004; Ganel et al., 2005; Kaufmann & Schweinberger, 2004). One can argue that the direction in which an interaction between two dimensions occurs depends on the relative speed with which each dimension is processed and/or on the relative dominance of each dimension for the cognitive system (for a discussion, see Garner, 1983).

1.2. Time course of facial identity and expression processing

Because of their fine temporal resolution, ERP studies have been designed to investigate the time course of face processing. Sensitivity to face configurations emerges as early as 80 ms after stimulus-onset with the P1 occipito-temporal component reflecting face detection (e.g., Herrmann, Ehlis, Ellgring, & Fallgatter, 2005). The P1 component is also an index of facial expression detection (e.g., Batty & Taylor, 2003). However, the first stage at which enough evidence is accumulated to identify an individual face is indexed by the N170 component appearing around 160 ms after stimulus-onset (for a review, see Rossion & Jacques, 2008; see also Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Jacques & Rossion, 2009 for more recent references). The discrimination between expressions can also be realized in the same time range, as indexed by an adaptation effect (i.e., reduction of the electrophysiological signal in response to stimulus repetition) on the N170 (e.g., Campanella, Quinet, Bruyer, Crommelinck, & Guerit, 2002). Thus, identity and expression may be processed during the same time course, as we found interactions between familiarity and expression appearing in the N170 time range for both familiarity and expression tasks (Leleu et al., 2010). Altogether, these results suggest that face dimensions are processed at the same speed. If so, one dimension may achieve dominance over the other (Garner, 1983). This intriguing question can be investigated with a paradigm that can reveal interactions and the relative dominance between two dimensions of the same object: task switching.

1.3. Asymmetric switch-cost to investigate dominance of facial identity

As in the Garner-type paradigm, task switching (i.e., task alternations allowing a switch-cost-longer response times (RTs) during switch compared to repeat trials, see Kiesel et al., 2010; Vandierendonck, Liefooghe, & Verbruggen, 2010 for recent reviews) can highlight interactions between two dimensions by manipulating selective attention at several levels of processing. Perceptual interactions can first be observed depending on the nature of the stimuli and their trial-to-trial relations. We used task switching with bivalent faces (i.e., same stimuli used in both tasks) and competitor priming (i.e., the irrelevant dimension in a switch trial being the same as the relevant one in the previous repeat trial) and showed interactions in early perceptual stages of visual processing as soon as the N170 component (Leleu et al., 2010), whereas no interaction occurred in other ERP studies where subjects performed the two tasks in separate sessions with randomly counterbalanced stimuli (e.g., Caharel et al., 2005). Secondly, executive interactions can be observed in task switching with response-based interference. When the same response-set is used to perform the two tasks (bivalent responseset), each motor response has different meanings depending on the task, allowing for congruency effects in executive control (e.g., Brass et al., 2003). Thirdly, interactions can be highlighted to a larger extent at the level of task sets, also called stimulus-response (S-R) mappings, and defined as the organization of mental representations and cognitive processes that enable to act in accordance with task requirements. Indeed, when participants perform two tasks alternatively, an active task-set reconfiguration occurs and is partly responsible for the switch-cost. It is interesting to note that when tasks differ in dominance, an interaction in the reconfiguration of task sets is indicated by a paradoxical asymmetric switch-cost (Allport & Wylie, 2000; Allport, Styles, & Hsieh, 1994; Barton, Greenzang, Hefter, Edelman, & Manoach, 2006; Meuter & Allport, 1999; Philipp, Gade, & Koch, 2007; Yeung & Monsell, 2003). This well-known effect was first reported by Allport et al. (1994) with Stroop tasks (Stroop, 1935), as costs were larger when switching toward the dominant and stronger color-word reading task than the non-dominant and weaker ink-color naming task, replicated since then (Allport & Wylie, 2000; Yeung & Monsell, 2003), but also occurring when switching between native and learned languages (Meuter & Allport, 1999; Philipp et al., 2007) or between saccades and antisaccades (e.g., Barton et al., 2006).

Hence, to investigate whether interactions between identity and expression are due to differences in dominance, we designed a taskswitching procedure whereby subjects performed familiarity and expression judgments. We sought to find a greater switch-cost in the familiarity than in the expression task. Because we did not find an asymmetric switch-cost in our previous task-switching study (Leleu et al., 2010), stimuli were randomly counterbalanced in the present experiment, expecting to enhance interaction in task sets. Indeed, because subjects were able to predict the irrelevant dimension in a switch trial, competitor priming in the previous research may have attenuated interaction in task sets and intensified interactions in perceptual representations of faces as we found in early visual ERP components. To clarify when interactions in reconfiguration of task sets start from along the processing stream, ERPs were also recorded. The aim was to discover correlates of asymmetric switchcosts by analyzing parieto-central P3 and fronto-lateral N2 components often investigated in the task-switching literature (e.g., Karayanidis, Coltheart, Michie, & Murphy, 2003; Poulsen, Luu, Davey, & Tucker, 2005), related to post-perceptual and executive processes associated with reconfiguration of task sets. We also analyzed occipito-temporal P1 and N170 components to investigate switchcosts at perceptual stages.

2. Materials and methods

2.1. Participants

Fifteen participants (8 women; mean age = 22.4, range 18.7–27.3 years) were included in the study. All participants were right-handed, had normal or corrected vision, and had no previous history of neuropsychiatric illness. Written informed consent was obtained from all participants prior to the experiments.

2.2. Stimuli

The stimuli were obtained from 20 photographs of well-known celebrities and 20 unknown faces, half of which had neutral expression and the other expressing disgust, fear, anger, or sadness. Therefore, we used two pictures for each identity, one neutral and one expressing an emotion, finally comprising 10 familiar expressive faces, 10 familiar neutral faces, 10 unknown expressive faces, and 10 unknown neutral faces. These stimuli were selected after a survey among 50 students, over 94% of whom correctly recognized the face (when needed) and the emotional expression. The images were calibrated at different levels of grey with a mean size of 6 cm × 8 cm and standardized for luminance and contrast with Adobe Photoshop® software.

2.3. Procedure

After electrode-cap placement, participants were seated in a quiet and dark room, at a viewing distance of 90 cm from the center of a computer screen, where faces were presented with full frontal view on a grey background and had a size of $3.8^{\circ} \times 5.1^{\circ}$ of visual angle. An original task-switching paradigm was used between facial familiarity and emotional expression tasks. It combined the presentation of a visual cue preceding each trial as in the "task-cueing" procedure (Meiran, 2000) and a predictable task-sequence as in the "alternating-runs" procedure (Rogers & Monsell, 1995). Participants were asked to judge in the familiarity task whether the face was known, and in the expression task whether the face expressed an emotion.

In each trial, a verbal visual cue lasting 50 ms indicated the nature of the task ("familiarity" or "expression"), followed by a fixation point

lasting 250 ms, before presentation of the stimulus (cue-target interval (CTI) of 300 ms). Each stimulus lasted 1000 ms and responses were recorded after stimulus-onset by pressing the right side of a computer mouse with the right thumb or the left side with the left thumb. To control response-based effects between tasks (e.g., Brass et al., 2003), associations between fingers and responses were randomized across tasks and participants. After each response, the screen went blank for a random duration between 1000 and 1500 ms (Fig. 1).

In each session, participants performed 32 blocks of 21 trials (672 trials). Consequently, each face (i.e., an identity associated with an emotion) was repeated 17 times, except for 8 faces not included in first trials (not analyzed, see after) and repeated 16 times. For each block, because the first trial was neither repeated nor switched, it was not comprised in the data analyses. Half the blocks started with the familiarity task as the first trial and the other half with the expression task. Blocks were randomized across participants. The first trial was followed by a repeat trial (the same task) and then by a switch trial (the other task), and so on (e.g., if the first trial comprised the familiarity task, the next repeat trial was the same task, the next switch trial being the expression task, see Fig. 1). Alternations of repeat and switch trials were presented with this predictable sequence. To control for stimulus-based effects (e.g., Leleu et al., 2010), faces were randomized across trials.

2.4. EEG recording

EEG was continuously recorded from 32 Ag/AgCl electrodes mounted in an electrode cap according to the 10-10 classification system. During EEG recording, all electrodes were referenced to a frontocentral one (AFz), and impedances were kept below 5 k Ω . EEG was amplified (resolution: .16 μ V; band-pass: high-pass with a 1 s time constant and low-pass equal to 100 Hz), digitalized at a 256 Hz sampling rate, and stored on a Deltamed system. Codes were synchronized to stimulus delivery and used for averaging sample epochs offline. After a 40 Hz low-pass filtering of the EEG, trials contaminated with eye movements or other artifacts ($\geq \pm\,100\,\mu$ V) and incorrect trials were rejected.

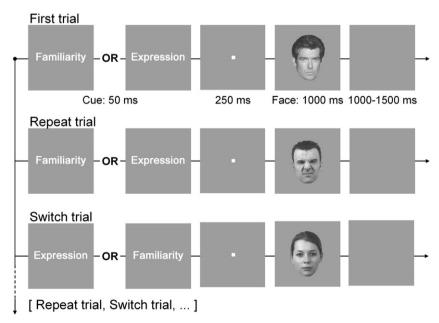


Fig. 1. Timeline of stimulus presentation. In each trial, a visual verbal cue giving the nature of the task was presented for 50 ms and followed by a fixation point for 250 ms. The face stimulus appeared for 1000 ms and a random duration between 1000 and 1500 ms appeared before the next trial. In each block of trials, participants performed a first trial, followed by a repeat trial of the same task and a switch trial of the other task. Participants alternated between repeat and switch trials until the end of the block.

2.5. Statistical analyses

Only RTs ranging between 300 and 1500 ms were taken into account. To investigate interactions in task sets, repeated-measure ANOVAs were performed for two main factors: Trial (repeat vs. switch), and Task (familiarity vs. expression).

ERPs extracted by averaging separate trials for each participant, experimental condition, and electrode, were stimulus-locked and averaged for 1250 ms, including a 250 ms baseline before stimulusonset and a 1 s interval after stimulus-onset. A common average reference was recalculated from the following 20 electrodes: F3, F4, F7, F8, C3, C4, CPz, Cz, Pz, Fz, T7, T8, TP7, TP8, P7, P8, P3, P4, CP3, and CP4 (Bertrand, Perrin, & Pernier, 1985). After visual inspection of the signals, ERP analyses were performed in sites where amplitudes were maximal (see Fig. 3): the P1 and the N170 at lateral occipitotemporal sites, the P3 at parieto-central sites, and the N2 at frontolateral sites. Statistical analyses comprised sites designated as occipito-temporal left (OTL: electrodes O1 and PO7), occipitotemporal right (OTR: electrodes O2 and PO8), parietal central (PC: electrodes Pz and CPz), frontal left (FL: electrodes F3, F7, and Fp1), and frontal right (FR: electrodes F4, F8, and Fp2). Mean amplitudes were calculated at a 75-150 ms time window for the P1 and 150-200 ms for the N170. Because P3 and N2 components were long waves with a 400 ms time course, mean amplitudes were also calculated at eight 50 ms-lasting time windows for these two components (from 200 to 600 ms). Repeated-measure ANOVAs were computed for each location with the same main factors as behavioral analyses (Trial and Task). Because of the eight time windows in the analyses of P3 and N2 components, the Window factor (8 modalities) was added in the corresponding ANOVAs. Greenhouse-Geisser corrections with adjusted degrees of freedom were applied for controlling type I errors, corresponding to the epsilon (ε) value (Keselman & Rogan, 1980). Post-hoc comparisons were performed with the Tukey HSD test whenever necessary (correction for multiple comparisons).

3. Results

3.1. Behavior

In error rates, a main effect of the Task (F(1,14) = 9.23, p = .009) showed that the familiarity task was performed with fewer errors (4.43 \pm .63% (standard error)) than the expression task (6.32 \pm .98%), indicating greater difficulty for expression processing. There was also a significant Trial effect in RTs (F(1,14) = 45.31, p < .001) with a classical switch-cost (i.e., more time needed to perform switch (883 \pm 51 ms) than repeat (791 \pm 46 ms) trials).

More importantly for our purpose, a significant interaction between Task and Trial appeared in RTs (F(1,14)=23.93, p<.001). Supporting our hypothesis, this interaction indicates an asymmetric switch-cost, as the Trial effect was more important in the familiarity (repeat: 767 ± 31 ms vs. switch: 906 ± 39 ms, F(1,14)=86.23, p<.001) than the expression (repeat: 815 ± 36 ms vs. switch: 859 ± 36 ms, F(1,14)=8.34, p=.012) task. Conversely, there was no such interaction for error rates (F(1,14)=.06, p=.81). Fig. 2 depicts the Task effect in error rates and the asymmetric switch-cost in RTs.

3.2. ERPs

Several sites on the scalp were taken into account: OTL (O1 and PO7), OTR (O2 and PO8), PC (Pz and CPz), FL (F3, F7, and Fp1), and FR (F4, F8, and Fp2). These electrodes and the corresponding signals depending on the task are displayed in Fig. 3. A significant main effect of the Task appeared in the P1 time range at OTL (F(1,14) = 21.31, p < .001) and OTR (F(1,14) = 12.45, p = .003) sites, with greater amplitudes for the familiarity (OTL: $4.50 \pm .99 \,\mu\text{V}$, OTR: $3.81 \pm 1.02 \,\mu\text{V}$) than the expression (OTL: $3.48 \pm .88 \,\mu\text{V}$, OTR: $2.80 \pm .74 \,\mu\text{V}$) task. No other effect was significant (p > .05) for this component. For the N170 component, no main effect or interaction achieved significance (p > .05).

Concerning the P3 component at the PC region, a significant Window×Trial interaction was found (F(2,31)=3.53, $\epsilon=.32$, p=.037). It was explained by the Trial effect significant in six time windows between 200 and 500 ms after stimulus-onset (200–250 ms time range: F(1,14)=5.17, p=.003; 250–500 ms time range: all F>18, p<.001, see Table 1 for detailed significant effects in both time windows). Amplitudes were enhanced for repeat relative to switch trials (averaged across time windows: repeat: $2.17\pm.49\,\mu\text{V}$ vs. switch: $1.44\pm.46\,\mu\text{V}$). Post-hoc comparisons between repeat and switch trials revealed a significant effect in the 200–250 ms time range for the expression task only (p=.033; familiarity task: p=.17) and in the 250–500 ms time range for the familiarity (all p<.01) and expression (all p<.01) tasks. No other effect was significant (p>.05) for this component.

At the level of the frontal N2 component, a significant Window x Task x Trial interaction appeared only in the left hemisphere (FL sites) (F(3,35)=5.95, $\epsilon=.36$, p=.003). At the 250–300 ms time window, there was a significant Trial effect (F(1,14)=5.90, p=.029), with greater amplitudes for repeat ($-3.21\pm.68\,\mu\text{V}$) than switch ($-2.72\pm.72\,\mu\text{V}$) trials. Most important in our goal of finding ERP correlates of greater switch-cost in the familiarity task, significant Task by Trial interactions were observed at five time windows in a 200–450 ms time range (all F>5.53, p<.035, see Table 1). In line with the greater switch-cost found for the familiarity task in RTs, these interactions were explained by a Trial effect only for the familiarity task (all F>9.58, p<.008, post-hoc analyses: all p<.01), with

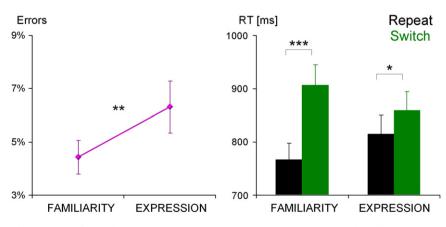


Fig. 2. Left: mean error rates elicited by the task performed (bars represent standard errors). Right: mean response times elicited by switch and repeat trials depending on the task (* p<.05; ** p<.01; *** p<.001). (For the interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

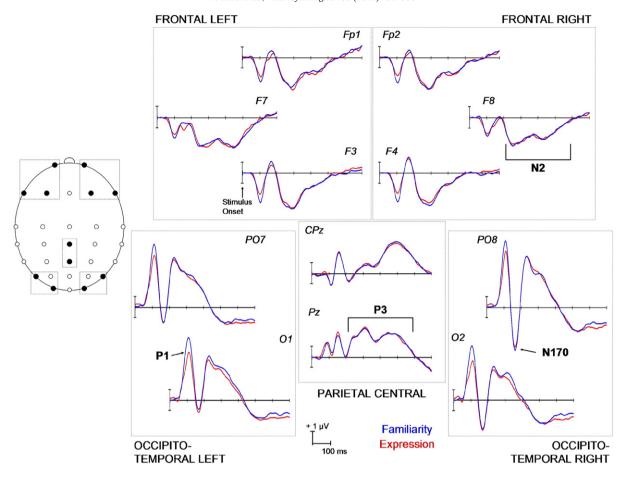


Fig. 3. Grand average ERP waveforms elicited by the familiarity and the expression tasks at 12 electrodes displayed on the scalp. Five frames represent the topographical sites included in statistical analyses and the P1, N170, P3 and N2 components are indicated on the O1, PO8, Pz and F8 electrodes respectively. (For the interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

more negative amplitudes for repeat (averaged across time windows: $-2.61\pm.43\,\mu\text{V}$) than switch $(-1.95\pm.44\,\mu\text{V})$ trials. Interestingly, there was no significant interaction between these factors (p>.05) in the right hemisphere (FR sites). Fig. 4 depicts ERP waveforms at FL, FR and PC sites depending on the trial in both tasks, and subtraction waveforms elicited by the difference between switch and repeat trials depending on the task.

4. Discussion

The purpose of the present study was to evaluate whether face identity is more dominant than emotional expression, investigated

Table 1 Main effects and interactions with Task and Trial factors for electrophysiological ANOVAs (OTL: occipito-temporal left; OTR: occipito-temporal right; PC: parietal central; FL: frontal left; *p<.05; **p<.01; ***p<.001).

ERP	Task	F	Trial	F	$Task{\times}Trial$	F
Time windows						
[75–150]	OTL OTR	21.31*** 12.45**				
[150-200]						
[200-250]			PC	5.17*	FL	5.54*
[250-300]			PC	41.19***	FL	31.72***
			FL	5.90*		
[300-350]			PC	28.32***	FL	6.46*
[350-400]			PC	21.98***	FL	10.07**
[400-450]			PC	32.77***	FL	9.14**
[450-500]			PC	18.72***		
[500-550]						
[550-600]						

at the level of reconfiguration of task sets during task switching between familiarity and expression judgments. The results support this hypothesis, as switch-cost in RTs (i.e., difference between switch and repeat trials) was greater in the familiarity than the expression task, assuming that asymmetric switch-cost is an index of the relative dominance of two task sets with a paradoxical greater cost when switching toward the dominant task. Critically, a neural correlate of this asymmetric switch-cost was found at the level of the frontal N2 ERP component in the left hemisphere. This electrophysiological effect suggests that the interaction occurs during top-down executive control processes as discussed in the following sections. We also provide some suggestions for future research.

$4.1. \, A symmetric \, switch-cost \, reveals \, the \, dominance \, of \, the \, familiarity \, task$

Several authors have considered an asymmetric overlap between face identity and emotional expression, as identity serves as a reference from which expressions are more easily but not exclusively derived (Ellamil et al., 2008; Fox et al., 2008, 2009; Ganel & Goshen-Gottstein, 2004; Ganel et al., 2005; Kaufmann & Schweinberger, 2004). To explain the direction in which this interaction occurs, we assessed whether identity dominates over emotional expression by manipulating selective attention with a task-switching paradigm, in which reconfiguration of task sets (i.e., perceptual and executive processes bound together in S–R mappings) allows a switch-cost (i.e., longer RTs in switch than repeat trials). Classically, a paradoxical asymmetric switch-cost is found with Stroop words, as greater cost is observed when switching toward the color-word reading task (e.g., Allport et al., 1994). Considering that this effect reflects the dominance of reading over color naming

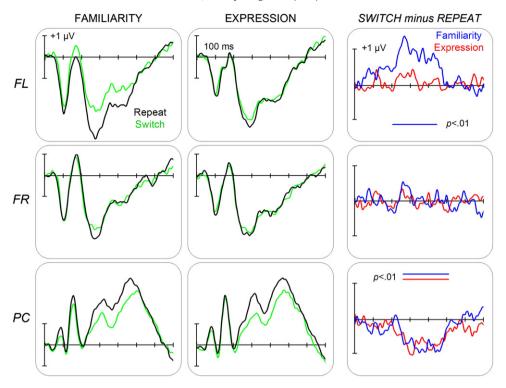


Fig. 4. Grand average ERP waveforms elicited by switch and repeat trials in the familiarity task (left) and in the expression task (middle column) at frontal left sites (top), frontal right sites (middle row) and parietal central sites (bottom). The right column depicts subtraction ERP waveforms elicited by the difference between switch and repeat trials for both tasks. Significant *post-hoc* comparisons (p<.01) between waveforms recorded in the switch versus repeat conditions are indicated as horizontal blue bars for the familiarity task and as red bars for the expression task (FL: frontal left; FR: frontal right; PC: parietal central; for the interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

(Allport & Wylie, 2000; Allport et al., 1994; Yeung & Monsell, 2003), our finding of larger switch-cost in the familiarity task indicates that identity is more dominant than expression during task switching. No switch-cost was observed in error rates, but the familiarity task was performed with fewer errors than the expression one. While this effect was found whatever the nature of trials (i.e., repeat or switch), it supports the idea that the familiarity task acts as the dominant one in this study, indexing an overall task-strength effect irrespective of task switching, as found in previous studies investigating asymmetric switch-cost (e.g., Yeung & Monsell, 2003).

To investigate why more time is needed to perform the dominant task helps us understand at which stage of processing the interaction occurs. One classical interpretation of switch-cost considers prolonged processing on switch trials due to long-term bottom-up positive and negative task-set priming from previous trials (e.g., Allport et al., 1994; Waszak, Hommel, & Allport, 2003, 2005; Wylie & Allport, 2000). Positive priming is defined as the persisting activation of the currently irrelevant task-set and negative priming as the persisting inhibition of the currently relevant task-set (but previously irrelevant). Allport and collaborators suggest that negative priming is responsible for the asymmetric switch-cost (Allport et al., 1994; Waszak et al., 2003, 2005; Wylie & Allport, 2000). Because the dominant task must be strongly inhibited when switching to the nondominant task, negative priming (which corresponds to this persisting inhibition) is naturally more active for the dominant task. On another account, switch-cost reflects the time taken by executive control processes to reconfigure the task-set, as top-down retuning of S-R mappings to perform the new task (e.g., Rogers & Monsell, 1995; Rubinstein, Meyer, & Evans, 2001). To explain asymmetric switch-cost, Yeung and Monsell (2003) developed a formal model assuming an interaction between task-strength, exogenous priming, and the active endogenous control process. Task-strength represents baseline activation, exogenous priming is modeled as a persistent increase of activation of the previous task-set (i.e., congruent priming during repeat trials and incongruent priming during switch trials), and the executive control process serves to increase the activation of the currently relevant task-set dynamically adjusted to the level of interaction. According to this model, asymmetric switch-cost appears because more control is needed when switching to the weaker task, resulting in faster RTs, than in switching to the stronger task for which the control process is less activated.

In summary, according to the first theory, the dominance of one task over the other is grounded in an interaction in bottom-up perceptual/post-perceptual processing of task-set, while the second theory rather suggests an interaction in top-down executive control processing modulated by task-strength and priming (for other accounts of switching assuming both endogenous control and exogenous priming, see Ruthruff, Remington, & Johnston, 2001; Sohn & Carlson, 2000; Yehene & Meiran, 2007). Thus, the time course of asymmetric switch-cost may differ depending at which stage of processing an interaction in task sets occurs.

4.2. Interaction in familiarity and expression task sets along the processing stream

A task effect occurred at the very first stage of processing, namely the P1 component, with amplitudes enhanced during the familiarity task. Although some authors assume that the P1 is the earliest face-sensitive response in visual ERPs (e.g., Herrmann et al., 2005), this wave is often related to low-level visual properties such as spatial frequency spectra, luminance, and contrast (Rossion & Jacques, 2008; Rousselet, Husk, Bennett, & Sekuler, 2008). However, the stimuli were the same for both tasks, and so low-level properties cannot account for the effect. Instead, the modulation of early selective attention may explain it, since changes in P1 amplitudes have been obtained during bottom-up spatial attention (Di Russo & Spinelli,

1999; Hopfinger & West, 2006), or top-down selective and non-selective attention (Clark & Hillyard, 1996; Fu, Fedota, Greenwood, & Parasuraman, 2010; Taylor, 2002). Attending to particular features of the face can influence activity in the cortical ventral stream, allowing inputs from attended brain regions to gain access to higher stages of perceptual analysis. In a trial, more resources may be engaged as early as cue-onset and may modulate subsequent P1 amplitudes. This process may be more efficiently done in the familiarity task due to its dominance. Hence, as for the effect of the task in error rates, larger P1 amplitudes appeared to reflect task-strength irrespective of task switching. This insensitivity to switch-cost further suggests that the interaction in task sets does not occur at this early perceptual stage of processing.

In the N170 time range, no significant effect was observed considering Task x Trial analyses. The only significant effects concerned familiarity (celebrities vs. unknown) and expression (negative vs. neutral), analyses not presented in this paper because they did not bring new interesting findings. Notably, the interactions between familiarity and expression factors at the level of the N170 observed in our previous study (Leleu et al., 2010) were not significant (p > .05). Because in the previous study competitor priming was used, permitting subjects to predict the irrelevant dimension in switch trials, it may have enhanced perceptual interactions, lacking when stimuli are randomly counterbalanced. These negative results further suggest that interactions may be observed at several levels of processing and modulated as a function of experimental requirements such as relations between subsequent stimuli, especially with high selective attentional load. Future research should investigate this interesting question.

At the level of the stimulus-locked P3 component at PC sites, switch trials had lower amplitudes than repeat trials irrespective of the task, confirming previous results (Barcelo, Munoz-Cespedes, Pozo, & Rubia, 2000; Goffaux, Phillips, Sinai, & Pushkar, 2006; Hsieh & Liu, 2008; Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010; Jamadar, Michie, & Karayanidis, 2010; Karayanidis et al., 2003; Nicholson, Karayanidis, Bumak, Poboka, & Michie, 2006; Periáñez & Barceló, 2009; Poulsen et al., 2005), especially when the task sequence is predictable (e.g., Swainson, Jackson, & Jackson, 2006). This effect has been attributed to competition or interference between stimulus representations (Barcelo et al., 2000; Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010; Wylie, Javitt, & Foxe, 2003), difficulty in target evaluation (Goffaux et al., 2006), task-set reconfiguration (Nicholson et al., 2006), task-set implementation (Periáñez & Barceló, 2009; Swainson et al., 2006), or to context ambiguity resulting in variations in updating (Hsieh & Liu, 2008). Whereas slightly different, all these assumptions are influenced by traditional interpretations of the P3 modulations such as context updating in working memory (Donchin & Coles, 1988) or priming effects depending on target evaluation (Azizian, Freitas, Watson, & Squires, 2006). Thus, our findings can be considered as a reduced positivity for switch trials due to incongruent priming from the previous trial (different task-set) resulting in increased competition or difficulty in stimulus evaluation (Barcelo et al., 2000; Goffaux et al., 2006; Wylie et al., 2003), or as an increased positivity for repeat trials (Jamadar, Michie, & Karayanidis, 2010; Swainson et al., 2006) due to a facilitated evaluation of the target explained by the congruent priming from the previous trial (same task-set). We cannot exactly determine which mechanism can better explain our data, but both interpretations suggest that the modulations of the P3 component reflect the persistent activation of the previous task-set, also called exogenous priming of task sets in Yeung and Monsell (2003).

Supporting this view, brain imaging studies indicate a role of the posterior parietal cortex (PPC) during task switching associated with stimulus-triggered switching of the attentional focus (Braver, Reynolds, & Donaldson, 2003; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Sohn, Ursu, Anderson, Stenger, & Carter, 2000),

or detecting conflict in stimulus representations (Liston, Matalon, Hare, Davidson, & Casey, 2006). Whereas ERPs cannot precisely localize neural activity, the P3 component may reflect PPC target-triggered processing as a consequence of bottom-up stimulus-driven functions (Braver et al., 2003; Coull, Frith, Büchel, & Nobre, 2000; Hedden & Gabrieli, 2010; Ruge et al., 2005; Wylie et al., 2003). However, centro-parietal switch minus repeat differential negativity has been linked with activity in cingulate gyrus using correlations with fMRI signal or dipole modeling (Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010). The authors suggest that this activity reflects the need for conflict monitoring during switch trials. They consider an exogenous stimulus-based interference because it appears even with long preparation intervals. Future studies must indicate from which neural substrate the modulations of P3 amplitudes originate, but findings likely indicate exogenous priming of the previous task-set, fitting well with Yeung and Monsell (2003). This switching effect on the P3 component is not related with the asymmetric switch-cost observed in behavior, indicating that the interaction between the two task sets does not occur at this post-perceptual stage of processing.

Conversely, the N2 component showed an asymmetric effect of switching at left frontal sites, as repeat and switch trials differed only in the familiarity task, mirroring its larger costs in RTs. Taskswitching studies have not provided consistent results for switchand repeat-related frontal negativities. Some authors report larger frontal negativities on switch trials (Lorist et al., 2000; Poulsen et al., 2005), others on repeat trials (Rushworth, Passingham, & Nobre, 2002), or else no difference was found despite changes in the P3 component (Karayanidis et al., 2003). These conflicting results likely indicate task-specific processes. Brunia and van Boxtel (2001) conclude that frontal negativities reflect the ongoing control exerted over selective attention, in line with the role of the prefrontal cortex (PFC) in goal-directed behavior (Aron, Monsell, Sahakian, & Robbins, 2004; Braver et al., 2003; Cutini et al., 2008; Dreher, Koechlin, Ali, & Grafman, 2002; Hedden & Gabrieli, 2010; Miller & Cohen, 2001; Ruge et al., 2005; Wylie et al., 2003). Most importantly, the left PFC was specifically associated with rule formation (Miller & Cohen, 2001), endogenous control processes (Dreher et al., 2002), transient aspects of task switching (Braver et al., 2003), top-down control of competition between task sets (Aron et al., 2004; Wylie et al., 2003), or interference resolution (Hedden & Gabrieli, 2010). Thus, the left-lateralized effect we observed may indicate variations in the endogenous control of task sets. Supporting this assumption, Lavric and collaborators found a switch minus repeat anterior positivity as early as 300 ms after stimulus-onset with sources in left dorsolateral PFC, interpreted as a correlate of task-set reconfiguration (Lavric, Mizon, & Monsell, 2008). Once again, this interpretation fits well with Yeung and Monsell (2003), as an asymmetric switch-cost arises because of less top-down control during the dominant task. Hence, the present results suggest that control was modulated during switch trials in the familiarity task to resolve the competition between task

The influence of negative priming (Allport et al., 1994; Waszak et al., 2003, 2005; Wylie & Allport, 2000) appears not to have been at work in our tasks, perhaps because activation and inhibition mechanisms are more related to right PFC (Aron et al., 2004; Hedden & Gabrieli, 2010). Nevertheless, our ERP findings are not sufficient for strongly stating lateralization effects. Moreover, Arbuthnott (2008) considers that an inhibition process should be added to Yeung and Monsell's model. Further studies manipulating inhibition and control processes must be designed with brain imaging and/or ERPs to investigate this outstanding question.

P3 and N2 components may be envisaged as correlates of frontoparietal (or fronto-cingulate) loops during task switching (Dove et al., 2000; Dreher et al., 2002; Hedden & Gabrieli, 2010; Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010; Lavric et al., 2008; Liston et al., 2006; Ruge et al., 2005; Rushworth et al., 2002; Sohn et al., 2000), with the P3 reflecting more activities in PPC or cingulate gyrus and the N2 in PFC. However, because they follow the same time course, it is also possible that these represent two sides of the same deflection with the same bilateral dipoles, as observed for cue-locked switch minus repeat posterior positivity and anterior negativity (Lavric et al., 2008). Nonetheless, condition-specific modulations of each wave suggest different sources, at least partly. Further exploration through source analysis should help clarify these scalp effects, but our results and those of others (Aron et al., 2004; Braver et al., 2003; Coull et al., 2000; Cutini et al., 2008; Dreher et al., 2002; Hedden & Gabrieli, 2010; Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010; Lavric et al., 2008; Miller & Cohen, 2001; Ruge et al., 2005; Wylie et al., 2003) mainly support differential effects indexing bottom-up processing for the P3 related to PPC or cingulate activities, and top-down control functions driven by the PFC for the N2.

5. Conclusion

The present study aimed at clarifying the dominance of facial identity over expression at the level of task sets investigated with task switching between familiarity and expression judgments. An asymmetric switch-cost was found with respect to RTs (i.e., greater difference between switch and repeat trials in the familiarity task) supporting this hypothesis when subjects alternate task sets under high attentional demand. This behavioral effect had a neural correlate in left frontal ERPs, indexing modulations of endogenous control of task sets during switching to the familiarity task. These results confirm asymmetric dependencies between identity and expression during face processing, as identity serves as a reference from which expression can be more easily derived (Ellamil et al., 2008; Fox et al., 2008, 2009; Ganel & Goshen-Gottstein, 2004; Ganel et al., 2005; Kaufmann & Schweinberger, 2004). The overlap between facial dimensions is explained by their relative dominance and appears at late processing during executive control. Future research must investigate whether interactions between identity and expression can be observed at different levels farther along the processing stream, and whether they can be modulated depending on experimental and cognitive factors, such as relations between subsequent stimuli or the recruitment of selective attention.

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