On the temporal organization of facial identity and expression analysis: Inferences from event-related brain potentials

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In the present study, behavioral and electrophysiological markers of information processing—the lateralized readiness potential, the N170, and the P300—were recorded in order to assess the functional and temporal organization of facial identity and expression processing. A two-choice go/no-go task was used in which facial expression (happy vs. angry) determined response hand and response execution depended on facial familiarity (familiar vs. unfamiliar). The duration of facial identity and expression processing was manipulated in separate experiments. Together, the present findings in measures of overt and covert response activation indicate that facial identity is analyzed in parallel with, and typically somewhat faster than, facial expression. These data support a parallel model of face perception that assumes partial output from facial identity and expression processes to motor activation processes.

Theoretical Background

Bruce and Young's (1986) classical model of face recognition assumes parallel processing of facial identity and expression within functionally independent processing pathways. According to this model, faces are initially processed at a common stage of structural encoding, after which processing bifurcates into the analysis of different aspects of the face, such as facial identity, expression, and speech. The facial identity pathway is assumed to rely on viewpoint- and expression-independent descriptions of faces that are stored in face recognition units (FRUs), which contain the structural codes of familiar faces. In the functionally independent expression pathway, processing of facial expression occurs in parallel with that within the identity pathway. The assumption of independent identity and expression pathways has received support from behavioral, neurophysiological, and brain-imaging studies (e.g., Bruce, 1986; Bruce & Young, 1986; Ellis, Young, & Flude, 1990; Hasselmo, Rolls, & Baylis, 1989; Sergeant, Ohta, Macdonald, & Zuck, 1994; Tranel, Damasio, & Damasio, 1988; Young, McWeeny, Hay, & Ellis, 1986; Young, Newcombe, & Haan, 1993). However, as we will outline in more detail below, more recent face perception studies have challenged, on various grounds, this assumption of parallel and independent processing pathways (see

Calder & Young, 2005; Martens, Leuthold, & Schweinberger, 2010). The present psychophysiological study further investigates this issue by examining the influence of task-related and stimulus-related factors on the processing of facial identity and expression.

Doubts about the parallel model of face perception and its assumption of independent identity and expression processing have originated from behavioral face perception studies using the Garner interference task (see Garner, 1976). In these studies, participants typically fail to ignore irrelevant variations in the identity or gender of faces when processing facial expression, but not vice versa (e.g., Atkinson, Tipples, Burt, & Young, 2005; Baudouin, Martin, Tiberghien, Verlut, & Franck, 2002; Schweinberger & Soukup, 1998). Schweinberger, Burton, and Kelly (1999) examined whether differences in the relative processing speed of the two face dimensions were responsible for this asymmetric Garner interference effect (see also Atkinson et al., 2005; Ganel & Goshen-Gottstein, 2004). To this end, they manipulated the time demands for facial identity and expression analysis, using faces that were morphed along happy–sad and familiar–unfamiliar dimensions. Critically, reaction time (RT) performance in the expression classification task was impeded by irrelevant variations in facial identity even for stimulus

conditions in which the classification of facial identity was more time consuming than that of facial expression. By contrast, irrelevant variations in facial expression did not interfere with identity classification. To explain this one-directional crosstalk from identity to expression perception, Schweinberger et al. (1999) suggested a parallel-contingent processing model in which facial expression analysis is dependent on identity information, yet processing of identity and expression temporally overlaps (but see Ganel & Goshen-Gottstein, 2004).

Other findings also suggest a certain degree of dependence between facial identity and facial expression processing. On the basis of the results of a computational study of face recognition using principal components analysis (Calder, Burton, Miller, Young, & Akamatsu, 2001), Calder and Young (2005) proposed that facial identity and expression are first coded in a single multidimensional representation system and only at a later stage are analyzed by more specialized higher level identity and expression processes. Within the facial representation system, the coding of facial identity and expression is not completely independent, since some components of facial variability code both facial dimensions. Using a face adaptation paradigm, Fox and Barton (2007; see also Ellamil, Susskind, & Anderson, 2008; Winston, Henson, Fine-Goulden, & Dolan, 2004) obtained evidence in favor of expression-invariant representations of facial identity and of identity-dependent, in addition to identity-invariant, representations of facial expression.

Finally, some event-related brain potential (ERP) studies have indicated that expression analysis may even precede the structural encoding of faces—hence, also challenging Bruce and Young's (1986) face perception model (e.g., Eimer & Holmes, 2002; Holmes, Vuilleumier, & Eimer, 2003; Münte et al., 1998; Potter & Parker, 1997; Williams, Palmer, & Liddell, 2006). For example, Eimer and Holmes reported an anterior negativity, peaking at about 120 msec (N120) after face presentation, to be smaller for fearful than for neutral faces. By contrast, the later peaking posterior N170 component (see Bentin, Allison, Puce, Perez, & McCarthy, 1996), which has been specifically associated with the structural encoding of faces (e.g., Bentin & Deouell, 2000; Eimer, 2000), was not affected by facial expression. A crucial limitation of these ERP studies, however, is that expression processing was studied in isolation, rather than together with that of facial identity. As a result, it is not possible to arrive at straightforward conclusions regarding the relative time course of integrated facial identity and expression processing and, hence, the cognitive architecture underlying face perception.

Most recently, we (Martens et al., 2010) therefore assessed the temporal organization of facial identity and expression analysis in a task that required the processing of both facial stimulus dimensions, thereby overcoming the limitation above with previous ERP work. Specifically, we used a hybrid two-choice RT go/no-go task in which RT measurement was supplemented by the recording of ERPs—in particular, the lateralized readiness potential (LRP) (see Coles, 1989; De Jong, Wierda, Mulder,

& Mulder, 1988; Eimer, 1998). The LRP is a continuous online measure of selective motor activation with a clear neuroanatomical origin within the primary motor cortex (see Leuthold & Jentzsch, 2002). It allows assessing the duration of premotoric and motoric processing time by determining the LRP onset in waveforms time locked either to the onset of the stimulus (S-LRP) or to the overt response (LRP-R) (see Leuthold, Sommer, & Ulrich, 1996; Osman, Moore, & Ulrich, 1995). Importantly, the S-LRP interval indicates the duration of premotoric processing, whereas the LRP-R interval indicates the duration of late motoric processes. A second important characteristic of the LRP is its independence from the execution of an overt response. Thus, an LRP is present not only on go trials, but also on no-go trials—that is, when participants first covertly activate a response that is subsequently withheld in a hybrid choice RT go/no-go task (e.g., Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1992).

The LRP has been successfully applied in previous chronometric studies to uncover the hidden architecture underlying different cognitive functions (Abdel Rahman, Sommer, & Schweinberger, 2002; Osman et al., 1992; Smid, Mulder, Mulder, & Brands, 1992; Van Turenout, Hagoort, & Brown, 1997, 1999). Taking advantage of this approach, we (Martens et al., 2010) conducted two ERP experiments using a hybrid choice RT go/no-go task in which facial identity (famous vs. unknown) determined response hand (left vs. right), whereas facial expression (happy vs. angry) determined response execution (go vs. no-go). In addition to the measurement of the LRP and other ERP components (N170, P300), crucially, the time demands of identity and expression processing were varied by attenuating or exaggerating certain characteristics of real faces, using the morphing technique (Beale & Keil, 1995; Benson & Perrett, 1991; Schweinberger et al., 1999; Young et al., 1997). In both experiments, RT and S-LRP interval indicated that famous faces are processed more quickly than unfamiliar faces. Assuming faster identity than expression processing (Schweinberger et al., 1999), we reasoned that if expression is processed in parallel with and independently of facial identity, as has been proposed by Bruce and Young (1986), the relative completion times of facial identity and expression analysis will be similar if the duration of identity processing increases but more dissimilar if the duration of expression processing increases. Schweinberger et al.'s (1999) contingent-parallel face perception model in its continuous version predicts that the duration of motor processing increases with the difficulty of identity or expression discriminations. Conversely, according to the discrete version of this contingent-parallel model, the duration of motor processing should remain unaffected by experimental manipulations (for more details, see Martens et al., 2010). The associated time differences between identity-driven hand activation and expression-driven response execution should be sensitively reflected by the LRP.

In fact, the LRP findings broadly supported a parallel architecture of face processing, although they suggested that expression analysis depends on identity information

for famous faces. Specifically, when an unfamiliar face was presented, the LRP–R interval was shorter for easy than for hard familiarity discriminations, and a no-go LRP was present. These results were clearly at odds with the predictions of the parallel-contingent model. In addition, this model could not account for the finding of a reliable no-go LRP for famous faces only when the discriminability of facial expressions was hard and not easy. By contrast, the parallel-independent model better accorded with these LRP findings, since only the absence of a no-go LRP for famous faces when familiarity discriminations were easy appears difficult to reconcile with this model. We therefore concluded that expression analysis depends on facial identity information; that is, information about expression is readily available for famous faces, supporting a parallel-dependent model of face perception. Identity-dependent processing of expression was also in line with the finding that N170 amplitude was sensitive to manipulations of facial identity, as well as the difficulty of expression and familiarity decisions. On the basis of N170 findings, we tentatively concluded that structural encoding has not yet bifurcated for identity and expression analysis at the stage of structural encoding, in line with the assumption of a single multidimensional face representation system (e.g., Calder et al., 2001).

Still, as we pointed out previously (see Martens et al., 2010), an important open issue arises from the possibility that the specific task requirements influenced the organization and time course of facial identity and expression processing. That is, in our previous study, go responses were three times more frequent than no-go responses. As a result, participants might have strategically prioritized the familiarity dimension (response hand decision) over the expression dimension (go/no-go decision), for example, by allocating initially more attention to the processing of facial identity than to the processing of expression. Another issue relates to our N170 amplitude findings that indicated an influence of expression discriminability (intensity) at the stage of structural encoding. However, stronger evidence for such an influence could be provided by studying expression-specific effects in combination with expression intensity effects on N170 amplitude. For example, Batty and Taylor (2003) found a larger N170 to fearful faces than to other expressions. In addition, using a gender discrimination task, Sprengelmeyer and Jentzsch (2006) found that the expression intensity of faces displaying anger, fear, and disgust increased a posterior negativity starting in the N170 time range. Leppänen, Kauppinen, Peltola, and Hietanen (2007) replicated the intensity effect for fearful faces in an emotion discrimination task but, in extension, found no intensity effect on N170 for happy faces. However, other studies failed to show expression-related effects on the N170 component. Thus, Eimer and Holmes (2002; see also Williams et al., 2006) found an earlier anterior N120 component to be of larger amplitude for fearful than for neutral faces, whereas Schupp et al. (2004) found that faces displaying an angry expression, as compared with faces with neutral and happy expressions, elicited an augmented early posterior negativity (EPN) between 200 and 300 msec after face onset and an enhanced

late positive complex (P300). It is important to note, however, that these ERP studies investigated expression processing in isolation. Hence, it is problematic to generalize these findings to task conditions in which facial identity and expression are jointly processed.

The Present Study

The aim of the present experiments was to address the issue of strategic influence on face processing by reversing (relative to the study by Martens et al., 2010) the assignment of facial identity and expression dimensions to hand and go/no-go decisions. Thus, participants were required to perform frequent left-/right-hand decisions on the basis of the outcome of the expression analysis, whereas go/no-go decisions were dependent on facial familiarity. For example, one group of participants was asked to press the left response key for a happy person and the right response key for an angry person, but only if the face displayed a famous person, and not if it displayed an unknown person. That is, depending on the outcome of these two decisions, a response was given with either the left or the right hand or not at all. The difficulty of facial identity and expression processing was manipulated in order to selectively influence the duration of these processes, thereby allowing us to infer the temporal organization of face perception from LRP effects. Also, we studied expression-specific effects (happy vs. angry) on different visual ERP components (N120, N170, EPN, P300) and the LRP in order to reveal possible influences on structural encoding, higher level perceptual categorization, and motor stages.

EXPERIMENT 1

Experiment 1 used the hybrid choice RT go/no-go task in combination with the manipulation of expression discriminability. To this end, either original or faces morphed along the expression dimension were presented. As in previous studies, we expected faster processing of happy than of angry faces (e.g., Billings, Harrison, & Alden, 1993), with P300 latency and the S–LRP interval to localize this happy face advantage at a premotoric processing stage (Leppänen, Tenhunen, & Hietanen, 2003). Also, regardless of possible strategic influences on the organization of face perception, all face-processing models predict the S–LRP interval to increase with the time demands for the expression decision, because a specific response hand is contingent upon this decision. Most important, however, if Martens et al.'s (2010) findings were specific to the demands of the go/no-go choice RT task employed, now that expression is given priority, activation within the motor stage should initially depend on information from expression analysis and only later on facial identity information. In this case, the parallel model predicts a longer LRP–R interval for easy than for hard expression decisions and, at least when the waiting time for the go/no-go decision is long, a no-go LRP for the easy expression condition (cf. Figures 1A and 1B). However, if relative completion times of facial identity and expression analysis are not influenced by task requirements, the LRP–R interval should not be influenced by experimental conditions, and the no-go

Figure 1. Schematic illustration of predicted effects of expression difficulty (easy vs. hard) on the lateralized readiness potential (LRP) in the two-choice go/no-go task for a parallel model (for faster expression than identity processing, A = easy vs. B = hard; for faster identity than expression processing [cf. Martens, Leuthold, & Schweinberger, 2010], B = easy vs. C = hard discrimination) and for Schweinberger, Burton, and Kelly's (1999) parallel-contingent model of face processing (D = easy vs. E = hard discrimination). For the latter model, the motor stage depicted with solid lines refers to the continuous version, whereas the motor stage depicted with broken lines refers to the discrete version.

LRP should be absent (cf. Figures 1B and 1C). Finally, Schweinberger et al.'s (1999) parallel-contingent model assumes that facial identity is always processed prior to facial expression. Accordingly, this model assumes, in its continuous information transmission version, that the LRP–R interval increases with expression difficulty, whereas the discrete version predicts that the experimental effect will influence only the S–LRP interval. In addition, a general prediction of the parallel-contingent model is that the no-go LRP is absent, because facial-identity-based information about response execution is always available before expression-based information about response hand (cf. Figures 1D and 1E).

Method

Participants

A total of 22 right-handed participants were tested and received payment for participation (£12). Two participants were excluded from data analyses, 1 because of excessive EEG artifacts on more than 30% of the trials (e.g., drifts and EEG activity exceeding $\pm 60 \mu V$), whereas another 1 aborted the experiment. All the participants included in the data analysis ($M = 22.4$ years of age, range = 19–39 years; 10 females) reported normal or corrected-to-normal vision and were right-handed.

Stimuli and Apparatus

Images of eight famous and eight unfamiliar faces, each in happy and angry expressions (for details about the stimulus set, see Martens et al., 2010), were edited using Adobe Photoshop (Version 7.0) to remove the background and convert them into 8-bit grayscale images, adjusted to brightness and contrast. The horizontal and vertical resolution of each photographic frame was 170×216 pixels (72 pixels/in.). In order to independently manipulate the salience of the expression of the face, each photograph was morphed, using Sierra Morph (Version 2.5) software. Each happy face was paired with the angry face of the same person. Morphing for each pair was performed within the identity dimension from happy to angry. Eight morphed images were created for each continuum by blending two faces in the following proportions: 100:0 (i.e., 100% Face 1 and 0% Face 2), 71.4:28.6, 28.6:71.4, and 0:100. In the following, we will refer to the morph levels with 100:0 and 0:100 proportions as *easy expression discriminations* and the morph levels with proportions of 71.4:29 and 29:71 as *hard expression discriminations*. Martens et al. demonstrated reliable difficulty effects for the recognition of the displayed expression in RT and accuracy between the easy and hard expression discriminations.

The stimuli were displayed using the Experimental Runtime Software (ERTS), Version 3.32 (Berisoft Corporation, 2000), on a 19-in. monitor with a viewing distance of 80 cm, which was assured by a fixed chinrest. Accordingly, the visual angle of the stimuli was $3.6^\circ \times 4.3^\circ$. The participants indicated their responses by pressing one of the two a priori assigned keys on the ERTS key panel, using the left/right index finger.

Procedure

Facial expression was manipulated in its discriminability and determined the response hand (left vs. right), whereas facial familiarity determined response execution and was always easy to perceive. The participants performed a two-choice go/no-go task. Half of the participants had to decide whether a presented face was happy or angry but to withhold the response for familiar faces, whereas the other participants were to withhold the response for unfamiliar faces. Go trials occurred with a probability of $p = .75$. Expression, expression difficulty, and go/no-go trials varied randomly. The assignment of expression to response hand/key was balanced within each participant.

A trial started with the presentation of a fixation cross at the center of the screen for 500 msec. Subsequently, the target was displayed for 1,500 msec. The next trial commenced with the presentation of the fixation cross 700 msec later. In total, 1,280 experimental trials (960 go trials and 320 no-go trials) were presented. Each of the eight famous and eight unfamiliar faces was randomly presented for a total of 80 times. Since the faces displayed either happy or angry expressions at one of two levels of discrimination difficulty, a total of 20 physically identical faces were shown throughout the course of the experiment, 15 times on go trials and 5 times on no-go trials. The experiment started with a block of 39 practice trials using the experimental stimuli and the timing of the main experiment, but in contrast to the test trials, feedback was provided after every practice trial. Subsequently, 10 experimental blocks followed, consisting of 64 trials each. One half of the participants responded to happy faces with a left-hand response and to angry faces with a right-hand response, whereas the expression-to-response-key assignment was reversed for the other half of the participants. After 640 trials, the key assignment was exchanged. Thus, the participants responding to the first 10 blocks with their left index finger to happy faces now responded with their right index finger to these stimuli. Another practice block of 39 trials was presented, followed by another 10 experimental blocks of 64 trials each.

Electrophysiological Recordings

Scalp voltages were recorded using a 10–20 system montage of 32 sintered Ag/AgCl electrodes mounted in an electrode cap (Easy Cap, Herrsching, Germany). C3 and C4 were exchanged for C3' and C4' electrodes, which were placed above left and right motor areas, respectively. The TP10 (right upper mastoid) electrode served as initial common reference, and a forehead electrode (AFz) served as the ground. All impedances were kept below 10 k Ω and were typically below 5 k Ω . The electrooculogram (EOG) was recorded with supra- and infraorbital electrodes and with electrodes on the external canthi. All signals were recorded with a band-pass from 0.05 to 40 Hz (–6 dB attenuation, 12 dB/octave) and were sampled at a rate of 250 Hz.

Offline, trials containing blinks were corrected using the adaptive artifact correction method of Brain Electromagnetic Source Analysis (BESA) software (Ille, Berg, & Scherg, 2002). EEG activity was rereferenced to an average mastoid reference. Trials with any EEG artifacts (exceeding $\pm 60 \mu\text{V}$, drifts, channel blockings) and trials with incorrect behavioral responses were removed from analysis. The analysis epoch of stimulus-synchronized ERP waveforms started 200 msec before target onset and lasted for a total duration of 1,200 msec. For response-locked ERPs, the 1,200-msec epoch started 1,000 msec before the response. EEG and EOG activity were averaged time locked to either stimulus or response onset.

In addition, for each participant and experimental condition, the LRP was calculated by subtracting the activity over the primary motor cortex ipsilateral to the response hand from the ERP at homologous contralateral recording sites, using the C3' and C4' electrodes. These difference waveforms were averaged across hands to eliminate any ERP activity unrelated to hand-specific motor activation (see Coles, 1989; Eimer, 1998), resulting in the LRP.

Data Analysis

Correct responses within the time window of 150–1,500 msec after target onset were taken into data analysis. Stimulus-locked

ERP waveforms were aligned to a 200-msec baseline prior stimulus onset. Peak latencies of the posterior N170 and P300 were measured at electrodes P10 and Pz, respectively, where these components were maximal. Peak amplitude of the anterior N120 was determined at electrodes F3 and F4, of the posterior P120 at O1 and O2, and of the posterior N170 at P9 and P10, whereas P300 peak amplitudes were measured at midline electrode sites Fz, Cz, and Pz. The mean amplitude of the EPN deflection was measured in the time interval from 200 to 300 msec at electrodes P9 and P10. LRP onsets were measured in low-pass filtered (5 Hz, 6 dB/octave) waveforms and were analyzed by applying the jackknife-based procedure suggested by Miller, Patterson, and Ulrich (2001) and Ulrich and Miller (2001). That is, 20 different grand average LRPs, each containing data from 19 participants, were computed for each of the experimental conditions by omitting from each grand average the data of a different participant. LRP onsets were determined in the waveform of each grand average. The stimulus-synchronized LRP waveform (S-LRP) was aligned to a 100-msec baseline immediately before stimulus onset. As in similar previous studies (e.g., Abdel Rahman & Sommer, 2003), the S-LRP onset was determined using an absolute criterion at the point of time at which the amplitude reached a value of $-0.75 \mu\text{V}$. Onsets in the response-synchronized LRP (LRP-R) waveforms were obtained using the same absolute LRP amplitude criterion ($-0.75 \mu\text{V}$), with waveforms aligned to a 100-msec baseline starting 700 msec before response onset.

Dependent variables were subjected to repeated measures ANOVAs using conservative F tests (Huynh & Feldt, 1976). LRP onset latency measures were submitted to ANOVAs with F values corrected as follows: $F_C = F/(n-1)^2$, where F_C denotes the corrected F value and n the number of participants (see Ulrich & Miller, 2001). The presence of the no-go LRP was assessed by measuring mean S-LRP amplitude on no-go trials in successive 50-msec time intervals starting 300 msec after stimulus onset. For each time window, a two-tailed t test was performed against zero, and the no-go LRP was considered to be present if the t test was significant ($p < .05$).

The repeated presentation of a limited set of faces might influence familiarity and expression analyses. Although we reasoned that any effect of repetition should be similar for familiar and unfamiliar faces under the conditions of the present study—that is, when repetitions are nonimmediate but occur at relatively small lags (see Goshen-Gottstein & Ganel, 2000; Pfütze, Sommer, & Schweinberger, 2002)—differential repetition effects on RTs for familiar and unfamiliar faces were reported by others at both very short (Schweinberger, Pfütze, & Sommer, 1995) and longer (Ellis et al., 1990) lags. A possible influence of repetition on processing was examined in the following way. For each of the two halves of the experiment separately, the number of face repetitions was categorized into five bins (for go trials, 1st–3rd, 4th–6th, 7th–9th, 10th–12th, and 13th–15th repetition; for no-go trials, 1st, 2nd, 3rd, 4th, and 5th repetition). In addition, it was coded whether a famous or an unfamiliar face determined the go response. Splitting up the ERP data for the additional factors repetition bin and experimental half (first vs. second) was not feasible, because this would have deteriorated the signal-to-noise ratio of ERPs.

Results

Behavioral Performance

RTs and error rates for go trials are presented in Table 1. A preliminary analysis indicated that the factor of experimental half did not influence behavioral performance, except for a main effect that indicated faster and more accurate responses in the second than in the first half of the experiment. Therefore, behavioral data were collapsed across this factor. Behavioral data for go trials and for no-go trials were submitted to separate mixed-factor ANOVAs with the between-subjects fac-

Table 1
Mean Reaction Times (RTs, in Milliseconds) and Choice Response
Accuracy (Acc., in Percentages) As a Function of Experiment
(Experiment 1 vs. Experiment 2), Expression (Happy vs. Angry),
Difficulty of Decisions, and RT Bin

	Bin	Happy				Angry			
		Easy		Hard		Easy		Hard	
		RT	Acc.	RT	Acc.	RT	Acc.	RT	Acc.
Experiment 1	1	781	98.4	817	96.6	808	97.6	858	90.3
	2	747	99.0	777	96.4	770	97.4	824	92.3
	3	730	98.4	764	97.8	740	98.0	802	91.8
	4	703	99.2	732	96.9	720	99.7	778	91.3
	5	685	99.5	722	97.6	707	99.1	757	92.2
	<i>M</i>	729	98.9	762	97.0	749	98.6	805	94.6
Experiment 2	1	778	98.8	810	99.0	812	97.5	739	97.7
	2	734	98.7	765	98.6	773	98.6	791	98.0
	3	740	97.4	770	99.1	755	98.8	802	98.0
	4	731	99.0	755	98.6	741	97.8	775	97.8
	5	713	99.2	738	98.7	736	97.7	765	99.0
	<i>M</i>	740	98.6	768	98.8	764	98.1	795	98.1

Note—Difficulty of expression decisions was manipulated in Experiment 1, whereas difficulty of familiarity decisions was manipulated in Experiment 2.

tor of go stimulus (familiar vs. unfamiliar) and with repeated measures on the variables of expression (happy vs. angry), difficulty of expression discrimination (easy vs. hard), and repetition (Bin 1 to Bin 5). RT on go trials did not reliably differ for the two go stimulus groups [$M(\text{familiar vs. unfamiliar}) = 744 \text{ vs. } 779 \text{ msec}$; $F < 1$] but was shorter for happy than for angry faces [$M = 746 \text{ vs. } 777 \text{ msec}$; $F(1,18) = 23.0, p < .001$] and for easy than for hard-to-discriminate expressions [$M = 738 \text{ vs. } 784 \text{ msec}$; $F(1,18) = 152.3, p < .001$] and decreased with increasing number of repetitions [$M(\text{Bin 1 to Bin 5}) = 817, 780, 758, 735, \text{ and } 716 \text{ msec}$; $F(4,72) = 60.3, p < .001$]. The expression $\times$ expression difficulty interaction [$F(1,18) = 17.7, p < .001$] indicated a stronger effect of expression difficulty for faces displaying angry than for those displaying happy expressions ($\Delta M = 58 \text{ vs. } 34 \text{ msec}$). No other effects approached significance (all $F_s < 2.9, p_s > .10$).

Error rates on go trials displayed a similar pattern as RT. The main effect of repetition was not significant [$M(\text{Bin 1 to Bin 5}) = 95.7\%, 96.4\%, 96.8\%, 96.7\%, \text{ and } 97.1\%$; $F = 1.1, p > .30$], whereas the main effects of expression [$M = 97.9\% \text{ vs. } 95.1\%$; $F(1,18) = 11.3, p < .01$] and expression difficulty [$M = 98.8\% \text{ vs. } 94.2\%$; $F(1,18) = 50.0, p < .001$] were significant. These main effects were further qualified by the interaction between expression and expression difficulty, which indicated a stronger effect of expression difficulty for angry than for happy faces [$\Delta M = 7.2\% \text{ vs. } 1.9\%$; $F(1,18) = 15.3, p < .01$]. On no-go trials, the participants were better at withholding the response to unfamiliar than to famous faces [$M = 99.6\% \text{ vs. } 96.8\%$; $F(1,18) = 8.1, p < .05$]. The go stimulus $\times$ expression interaction [$F(1,18) = 5.9, p < .05$] was due to more accurate no-go performance in the group responding to the unfamiliar face if it had a happy than if it had an angry facial expression ($M = 97.6\% \text{ vs. } 96.2\%$).

Electrophysiological Measures

Lateralized readiness potential. The stimulus-synchronized LRP waveforms are depicted in Figure 2. LRP onset measures were submitted to an ANOVA with repeated measures on the variables of expression (happy vs. angry) and difficulty of expression discrimination (easy vs. hard). S-LRP onset to go trials occurred reliably earlier for easy than for hard expression discriminations [$M = 466 \text{ vs. } 493 \text{ msec}$; $F_C(1,19) = 4.6, p < .05$], whereas the main effect of expression [$M(\text{happy vs. angry}) = 464 \text{ vs. } 495 \text{ msec}$; $F_C(1,19) = 2.6, p > .12$] and the expression $\times$ discrimination difficulty interaction were not significant [$F_C(1,19) = 1.6, p > .22$]. As can be seen in Figure 3, the LRP-R interval was not reliably influenced by experimental variables ($M = 227 \text{ msec}$; all $F_Cs < 1.3, p_s > .26$).

Figure 2 (bottom) depicts the no-go LRP, which did not reliably differ from baseline at the time of go LRP onset and for four successive 50-msec periods thereafter ($-1.4 < t_s < 1.4, p_s > .16$). Separate t test analyses for participants responding to famous versus unfamiliar faces did not reveal a reliable no-go LRP in any of the experimental conditions and time intervals.

Anterior N120 and posterior P120. N120 and P120 peak amplitude values were submitted to a mixed ANOVA with the between-subjects factor of go stimulus (familiar vs. unfamiliar) and with repeated measures on the variables of go/no-go (go vs. no-go trial), expression (happy vs. angry), difficulty of expression discrimination (easy vs. hard), and electrode (F3 vs. F4 and O1 vs. O2, respectively). Note that a significant go stimulus $\times$ go/no-go interaction points to an influence of facial familiarity, due to the fact that one participant group produced go responses to famous faces and the other group to unfamiliar faces. Anterior N120 and posterior P120 deflections were not influenced by experimental variables (all $F_s < 2.85, p_s > .10$), except for a significant go stimulus $\times$ go/no-go $\times$ expression interaction in the analysis of the

Figure 2. Grand mean stimulus-locked lateralized readiness potential to go (top) and no-go (bottom) trials in Experiment 1 as a function of facial expression (happy vs. angry) and expression difficulty (easy vs. hard). The happy-easy go condition (thin black line) is depicted for comparison. S, stimulus onset.

Figure 3. Grand mean response-locked lateralized readiness potential (S-LRP and LRP-R, respectively) on go trials in Experiment 1 as a function of facial expression (happy vs. angry) and expression difficulty (easy vs. hard). R, response onset.

Figure 4. Grand mean stimulus-locked event-related brain potential (ERP) waveforms at the P10 (top) and Pz (bottom) electrodes on go trials in Experiment 1 as a function of facial expression (happy vs. angry) and expression difficulty (easy vs. hard). S, stimulus onset.

P120 [$F(1,18) = 5.9, p < .05$], indicating a larger P120 amplitude for famous-happy than for unfamiliar-happy faces ($M = 7.7$ vs. $7.3 \mu V$).

Posterior N170. Figure 4 (top) depicts stimulus-locked ERP waveforms at electrode P10, at which N170 was most pronounced, and Figure 5 depicts the topographic maps of ERP difference waveforms reflecting experimental effects. N170 peak amplitudes were analyzed with an identical ANOVA, except for the variable electrode (P9 vs. P10). N170 peak amplitude was larger over the right than over the left parieto-temporal electrode [$M = -7.9$ vs. $-6.2 \mu V$; $F(1,18) = 6.1, p < .05$] and larger for angry than for happy [$M = -7.3$ vs. $-6.9 \mu V$; $F(1,18) = 47.8, p < .001$] facial expressions. The significant go/no-go $\times$ expression interaction [$F(1,18) = 4.6, p < .05$] indicated a stronger expression effect on no-go than on go trials. The go stimulus $\times$ go/no-go interaction was not reliable ($F < 1$); however, the go stimulus $\times$ go/no-go $\times$ expression interaction approached significance [$F(1,18) = 3.8, p < .07$]. The group for which unfamiliar faces determined go responses showed a slightly larger expression effect in N170 amplitude on no-go trials than on go trials

($\Delta M = 0.6$ vs. $0.1 \mu V$)—that is, when faces were familiar. Although the go/no-go $\times$ expression difficulty interaction was not significant [$F(1,18) = 2.6, p = .12$], further testing revealed that on go trials, N170 amplitude was reliably larger for easy than for hard expression discriminations [$M = -7.2$ vs. $-7.0 \mu V$; $F(1,18) = 12.6, p < .01$]. N170 latency ($M = 191$ msec) was not influenced by experimental variables (all F s $< 2.2, p$ s $> .15$).

EPN. An analysis of mean EPN amplitudes (200–300 msec) analogous to those for N170 indicated a larger negativity for angry than for happy expression [$M = -4.4$ vs. $-4.0 \mu V$; $F(1,18) = 18.5, p < .001$] and for easy than for hard discrimination [$M = -4.4$ vs. $4.1 \mu V$; $F(1,18) = 28.8, p < .001$] conditions. The variables of go stimulus, go/no-go, and electrode did not produce significant effects (F s $< 2.85, p$ s $> .11$).

P300. Figure 4 (bottom) shows stimulus-locked ERP waveforms at electrode Pz. The analysis of P300 peak amplitudes with an identical ANOVA, except for the variable electrode (Fz, Cz, Pz), revealed a centroparietal distribution [$F(2,38) = 123.9, p < .001, \epsilon = .83$]. As can be seen in Figure 4, P300 amplitude was larger for easy than for

Figure 5. Spline-interpolated topographic maps of mean event-related brain potential (ERP) difference waveforms reflecting the expression effect (angry minus happy; left) and the expression difficulty effect (hard minus easy, right) for ERP components N170, EPN, and P300. Isopotential line spacing is $0.1 \mu\text{V}$.

hard expression discrimination conditions [$M = 5.4$ vs. $4.6 \mu\text{V}$; $F(1,18) = 16.0$, $p < .001$] and for angry than for happy expressions [$M = 5.5$ vs. $5.3 \mu\text{V}$; $F(1,18) = 4.2$, $p < .06$]. The latter expression effect was more pronounced over centroparietal electrodes [$F(2,36) = 6.2$, $p < .01$, $\epsilon = .88$; see Figure 5]. P300 amplitude was not reliably larger for go than for no-go trials overall [$M = 5.7$ vs. $5.0 \mu\text{V}$; $F(1,18) = 17$, $p > .20$]; however, the go/no-go $\times$ electrode interaction [$F(2,36) = 16.7$, $p < .001$, $\epsilon = .99$] indicated a relatively stronger positivity over the Cz electrode on no-go trials than on go trials. The go stimulus $\times$ go/no-go interaction produced a trend [$F(1,18) = 3.4$, $p < .09$], indicating a slightly larger P300 when famous faces, rather than unfamiliar faces, determined the no-go response ($M = 6.9$ vs. $4.7 \mu\text{V}$).

P300 latency was not reliably influenced by expression difficulty as a main effect ($F < 1$). The significant go stimulus $\times$ go/no-go $\times$ expression interaction [$F(1,18) = 5.1$, $p < .05$] indicated that P300 peaked earlier for happy than for angry facial expressions when famous faces determined the go response ($M = 509$ vs. 540 msec). No other effects were significant (all F s < 1.8 , p s $> .19$).

Discussion

The key findings of Experiment 1 relate to the effect of expression and expression difficulty on information processing as revealed by RT and electrophysiological indices. It is worth mentioning first that, in RT, these experimental effects were not influenced by the number of repetitions of an individual face or by the type of go stimulus (famous vs. unfamiliar), suggesting that repetitions generally speeded up facial expression and identity analyses. The expression effect on RT is consistent with previous reports of an advantage for happy faces, as compared with angry faces (e.g., Billings et al., 1993; Leppänen et al., 2003). Whereas the happy face advantage in the S-LRP interval was not statistically reliable, P300 latency on go trials showed a reliable expression effect for famous faces, hence providing further support for the view that expression influences the duration of

a high-level cognitive yet premotoric process (see Leppänen et al., 2003).

It is also important to point out that N170 amplitude was larger for angry than for happy faces, in line with other reports of an enlarged N170 for negative expressions (e.g., Batty & Taylor, 2003), an effect that appeared to be larger for famous than for unfamiliar faces. One interpretation of this finding is that structural encoding is influenced by expression, just not in its time demand, although it is also possible that angry faces more effectively capture attention (e.g., Fox et al., 2000). In addition, EPN and P300 amplitude were enhanced for angry, as compared with happy, faces, consistent with similar findings of Schupp et al. (2004). Moreover, N170, EPN, and P300 amplitudes were larger for easy than for hard expression discriminations—that is, when expression intensity was high rather than low. Also, the larger P300 to famous than to unfamiliar faces is consistent with previous reports (see Martens et al., 2010). Assuming that experimental effects on lower level sensory analysis can be excluded due to the absence of expression and difficulty effects on anterior N120 and posterior P120 components, except for the larger P120 to famous than to unfamiliar faces with happy expression, the present ERP amplitude findings indicate that expression intensity affected processing demands within structural encoding and higher level perceptual categorization stages. We will refer to further implications of these results in the General Discussion section.

More important regarding the temporal organization of face perception, RT indicated faster responses for easy than for hard expression discriminations, and this effect was slightly larger for angry than for happy faces. Since performance was better for easy than for hard expression conditions, differences in speed-accuracy trade-off across experimental conditions cannot account for the present RT data. Crucially, the analysis of LRP indices revealed an effect pattern that allowed us to evaluate the time course of facial identity and expression processing. The key findings were the following: (1) The time interval

from stimulus onset to the onset of the LRP was longer (27 msec) for hard than for easy expression discriminations, (2) the LRP–R interval was not reliably influenced by experimental conditions, and (3) a no-go LRP was absent. The effect of expression difficulty on the S–LRP interval reflected the one found in RT (46 msec). The absence of such an effect on N170 latency and P300 latency but its presence on the S–LRP interval suggests a locus of this effect at a postperceptual yet premotoric decision stage. The fact that the LRP–R interval was clearly uninfluenced by expression discriminability and also that the no-go LRP was absent speaks against a parallel model in which facial expression is analyzed more quickly than facial identity (Figures 1A and 1B). That is, such a model predicts a longer LRP–R interval for easy than for hard expression discriminations and a no-go LRP whenever there is a waiting time for the facial identity-related go/no-go decision. Consequently, we conclude that present LRP results indicate that changes in task requirements, with priority allocated to the analysis of expression, did not change the time course of elementary face perception processes. That is, the present LRP results are consistent with a parallel model with earlier output to motor-related processing from facial identity analysis than from expression analysis.

However, the parallel-contingent face perception model of Schweinberger et al. (1999) also assumes faster facial identity than expression processing. Can this model account for the present LRP findings? The increase of the S–LRP interval with expression difficulty, as well as the absence of the no-go LRP, is in line with this model. However, to account for the absence of a difficulty effect on the LRP–R interval, one has to assume that a response is activated only after the analysis of facial expression has been completed. This assumption implies that informa-

tion transmission from the expression stage to response-related stages is fully discrete, rather than continuous (see Figures 1D and 1C). Since this possibility cannot be ruled out on the basis of Experiment 1, we therefore manipulated, in Experiment 2, the duration of facial identity analysis to test the predictions of the parallel face perception model against those of the parallel-contingent model with discrete output to response-related stages.

EXPERIMENT 2

As in Experiment 1, facial expression determined response hand, whereas response execution depended on facial familiarity. However, the difficulty of facial identity (rather than expression) perception was manipulated by using faces morphed along the famous–unfamiliar dimension. The parallel model would be substantiated if the S–LRP interval is uninfluenced by the time demands of the identity decision. This is because the expression analysis determines the start of selective hand activation and this process is neither varied in difficulty nor dependent on the processing of identity. In addition, if processing of facial identity is faster than that of facial expression, as indicated by the results of Experiment 1 and our previous work (Martens et al., 2010), one should expect a shorter LRP–R interval for easy than for hard familiarity discriminations (see Figures 6A and 6B). In addition, a no-go LRP may be observed in the more difficult discrimination condition, due to the extended waiting time until the go/no-go decision. By contrast, the parallel-contingent model with discrete output to response stages predicts an influence of decision difficulty on the S–LRP onset and none on motor-related processing; that is, the LRP–R interval should be invariant and the no-go LRP absent (cf. Figures 6C and 6D).

Figure 6. Schematic illustration of facial-identity- and expression-processing models with the predicted difficulty effects of identity duration on the lateralized readiness potential (LRP) in the two-choice go/no-go task. A (easy) and B (hard): Parallel face perception model. C (easy) and D (hard): Parallel-contingent discrete processing model with discrete output to motor processing.

Method

Participants

Of 18 tested participants, 2 were excluded from data analysis because of excessive EEG artifacts (>30%). The remaining 16 participants ($M = 22.2$ years of age, range = 19–26 years; 11 female) were paid for participation (£12). All the participants were right-handed and reported normal or corrected-to-normal vision.

Stimuli and Apparatus

The stimuli and apparatus were identical to those in Experiment 1, with the exception that faces were morphed along the familiarity (famous–unfamiliar) dimension.

Procedure

The procedure was equivalent to that in Experiment 1, except that facial familiarity was manipulated in difficulty instead of expression discrimination.

Electrophysiological Recording and Data Analysis

Recording and data analysis methods were identical to those in Experiment 1.

Data Analysis

All aspects of data analysis were identical to those performed in Experiment 1, except that repeated measures included the variable of familiarity difficulty, rather than expression difficulty. It is worth noting that preliminary analyses of behavioral data, analogous to the one performed in Experiment 1, indicated faster and more accurate responses in the second than in the first half of the experiment. However, since experimental half (first vs. second) did not interact with the other experimental variables, behavioral data were collapsed across this factor.

Results

Behavioral Performance

RTs and error rates for go trials are presented in Table 1. Behavioral data for go trials and for no-go trials were submitted to separate mixed-factor ANOVAs with the between-subjects factor of go stimulus (famous vs. unfamiliar) and with repeated measures on the variables of expression (happy vs. angry), difficulty of familiarity discrimination (easy vs. hard), and repetition (Bin 1 to Bin 5). Responses were faster for happy faces than for angry faces [$M = 754$ vs. 779 msec; $F(1,14) = 26.1$, $p < .001$] and for easy than for hard-to-discriminate faces [$M = 751$ vs. 781 msec; $F(1,14) = 81.0$, $p < .001$] and decreased with increasing number of repetitions [$M(\text{Bin 1 to Bin 5}) = 810, 765, 767, 751$, and 738 msec; $F(4,56) = 31.6$, $p < .001$]. The go stimulus $\times$ familiarity difficulty interaction was significant [$F(1,14) = 5.7$, $p < .05$], whereas the group $\times$ expression interaction was a trend [$F(1,14) = 3.7$, $p > .05$]. The difficulty and expression effects were larger for the group responding to familiar faces ($\Delta M = 37$ and 35 msec, respectively) than for the group responding to unfamiliar faces ($\Delta M = 22$ and 16 msec, respectively). No other interactions were significant (all F s < 1.65 , $ps > .18$).

The analysis of error rates on go trials showed more accurate responses to faces displaying happy rather than angry expression [$M = 98.7\%$ vs. 98.0% ; $F(1,14) = 6.7$, $p < .05$]. The effect of repetition was not significant ($F < 1$). An identical analysis of accuracy on no-go trials indicated better performance for happy than for angry

faces ($M = 96.3\%$ vs. 93.6%), and for easy than for hard familiarity decisions ($M = 97.8\%$ vs. 92.2%) and when unfamiliar rather than famous faces determined the no-go response [$M = 97.5\%$ vs. 92.5% ; all F s(1,14) > 7.0 , $ps < .05$]. None of the effects including the variable repetition were significant (all F s < 1.75 , $ps > .17$). However, the go stimulus $\times$ expression $\times$ familiarity difficulty interaction was significant [$F(1,14) = 7.6$, $p < .05$]; when familiar faces determined the no-go response, there was a larger difficulty effect for angry than for happy faces ($\Delta M = 11.7\%$ vs. 6.9%).

Electrophysiological Measures

Lateralized readiness potential. Figure 7 depicts the stimulus-locked LRP waveforms for the different experimental conditions on go trials and no-go trials. LRP onset measures were submitted to ANOVAs with repeated measures on the variables of expression (happy vs. angry) and difficulty of familiarity discrimination (easy vs. hard). The S–LRP interval on go trials ($M = 448$ msec) was unaffected by expression and discrimination difficulty (all F cs < 1). Figure 8 depicts the response-locked LRP waveforms. The analysis of the LRP–R interval revealed a shorter LRP–R interval for easy than for hard familiarity decisions [$M = 207$ vs. 228 msec; $F_C(1,15) = 4.2$, $p = .058$]. The main effect of expression and the expression $\times$ familiarity difficulty interaction were not significant (all F cs < 1). As can be seen in Figure 7 (bottom), the no-go LRP did not reliably differ from baseline ($-1.0 < ts < 1.2$, $ps > .26$).

Anterior N120 and posterior P120. N120 and P120 peak amplitude values were submitted to an ANOVA with repeated measures on the variables of go stimulus, go/no-go (go vs. no-go trials), expression (happy vs. angry), difficulty of familiarity discrimination (easy vs. hard), and electrode (F3 vs. F4 and O1 vs. O2). The anterior N120 was not reliably influenced by experimental variables (all F s < 3.6 , $ps > .07$). The posterior P120 amplitude was larger for happy than for angry faces [$M = 9.4$ vs. $8.7 \mu\text{V}$; $F(1,14) = 8.7$, $p < .01$]. Moreover, there was a significant go stimulus $\times$ go/no-go $\times$ expression $\times$ familiarity difficulty interaction [$F(1,14) = 7.8$, $p < .05$], which was due mainly to a reverse expression effect in the group for which easy-to-discriminate famous faces determined the no-go response ($M = 7.9$ vs. $8.5 \mu\text{V}$).

Posterior N170. Figure 9 (top) depicts stimulus-locked ERP waveforms at electrode P10, at which N170 was most pronounced, and Figure 10 depicts the topographic maps of ERP difference waveforms reflecting experimental effects. In an identical ANOVA, except for the electrode variable (P9 vs. P10), it appeared that N170 amplitude was larger over the right than over the left parieto-occipital electrode [$M = -10.3$ vs. $-7.8 \mu\text{V}$; $F(1,14) = 11.1$, $p < .01$; see Figure 10], for angry than for happy expressions [$M = -9.4$ vs. $-8.7 \mu\text{V}$; $F(1,14) = 18.5$, $p < .01$], and for easy than for hard familiarity discriminations [$M = -9.1$ vs. $-8.9 \mu\text{V}$; $F(1,14) = 5.7$, $p < .05$]. The expression effect tended to be stronger over the right than over the left hemisphere [$F(1,14) = 3.3$, $p < .10$]. The go stimulus $\times$ go/no-go interaction was significant [$F(1,18) = 11.7$,

Figure 7. Grand mean stimulus-locked lateralized readiness potential on go (top) and no-go (bottom) trials in Experiment 2 as a function of facial expression (happy vs. angry) and familiarity difficulty (easy vs. hard). The happy-easy go condition (thin black line) is depicted for comparison. S, stimulus onset.

Figure 8. Grand mean response-locked lateralized readiness potential (S-LRP and LRP-R, respectively) on go trials in Experiment 2 as a function of facial expression (happy vs. angry) and familiarity difficulty (easy vs. hard). R, response onset.

Figure 9. Grand mean stimulus-locked event-related brain potential (ERP) waveforms at the P10 (top) and Pz (bottom) electrodes on go trials in Experiment 2 as a function of facial expression (happy vs. angry) and familiarity difficulty (easy vs. hard). S, stimulus onset.

$p < .01$], suggesting a familiarity effect in the sense that N170 was more negative for famous faces than for unfamiliar faces ($M = -9.3$ vs. $-8.8 \mu V$). The significant go stimulus $\times$ go/no-go $\times$ emotion $\times$ familiarity difficulty interaction [$F(1,14) = 7.8, p < .05$] was due mainly to an absent expression effect for unfamiliar faces that were hard to discriminate. No other experimental effects were significant (all F s $< 2.4, ps > .14$). N170 latency ($M = 182$ msec) was not influenced by experimental variables (all F s $< 2.3, ps > .16$).

EPN. An identical analysis of mean EPN amplitudes (200–300 msec) indicated larger negativity for angry than for happy expression [$M = -5.6$ vs. $-5.0 \mu V$; $F(1,14) = 21.6, p < .001$] and for easy than for hard conditions [$M = -5.4$ vs. $-5.1 \mu V$; $F(1,14) = 4.5, p < .05$]. The go stimulus $\times$ go/no-go interaction was significant [$F(1,14) = 19.6, p < .001$], indicating a larger EPN for famous than for unfamiliar faces ($M = -5.5$ vs. $-5.0 \mu V$). The significant go/no-go $\times$ difficulty $\times$ electrode interaction [$F(1,14) = 6.9, p < .05$] was due to the fact that on no-go trials, the difficulty effect was present only at the P10

electrode. No other effects were significant (all F s $< 2.8, ps > .12$).

P300. Figure 9 (bottom) shows the ERP waveforms at the Pz electrode, where P300 effects (see Figure 10) were most pronounced. The analysis of P300 peak amplitudes with an identical ANOVA, except for the electrode variable (Fz, Cz, Pz), revealed a centroparietal distribution [$F(2,28) = 57.8, p < .001, \epsilon = .89$]. The go/no-go $\times$ electrode interaction [$F(2,28) = 12.1, p < .001, \epsilon = 1.0$] indicated the ERP waveform to be more positive over frontocentral electrodes on no-go than on go trials. P300 amplitude was larger for easy than for hard discriminations [$M = 7.1$ vs. $6.2 \mu V$; $F(1,14) = 12.8, p < .01$]. This difficulty effect was more pronounced over the centroparietal electrodes [$F(2,28) = 8.6, p < .001, \epsilon = 1.0$] and here was stronger for no-go than for go trials, as indicated by the significant go/no-go $\times$ difficulty $\times$ electrode interaction [$F(2,28) = 5.3, p < .05, \epsilon = 1.0$]. The go stimulus $\times$ go/no-go interaction was significant [$F(1,14) = 6.3, p < .05$], indicating a larger P300 for famous than for unfamiliar faces ($M = 7.2$ vs. $6.1 \mu V$). Expression did not

Figure 10. Spline-interpolated topographic maps of mean event-related brain potential (ERP) difference waveforms reflecting the expression effect (angry minus happy; left) and the familiarity difficulty effect (hard minus easy; right) for ERP components N170, EPN, and P300. Isopotential line spacing is 0.1 μ V.

influence P300 amplitude as a main effect ($F < 1$). There was a significant go stimulus $\times$ familiarity difficulty $\times$ expression $\times$ electrode interaction, but further analysis indicated no reliable expression-related effects. The analysis of P300 latency ($M = 533$ msec) revealed no reliable experimental effects (all F s < 1.7 , p s $> .21$).

Discussion

Experiment 2 replicated the finding of shorter RTs with increasing number of repetitions and additionally revealed larger facial expression and familiarity difficulty effects for familiar faces, whereas repetition had no modulating influence. Crucially, RTs were generally shorter for happy than for angry faces (e.g., Billings et al., 1993; Leppänen et al., 2003), whereas S-LRP onset and N170 and P300 latency were all uninfluenced by facial expression. We have no ready explanation for the absence of the happy face advantage in chronometric ERP measures, except that effect size and power were lower than in Experiment 1, thus making it less likely to reliably detect this effect. As in Experiment 1, the anterior N120 was unaffected by expression. The posterior P120 was of larger amplitude for happy than for angry faces, except in one condition, when easy-to-discriminate famous faces determined the no-go response. Thus, P120 results suggest an expression effect on early sensory encoding. Crucially, posterior N170 amplitude was larger for angry than for happy faces and for famous than for unfamiliar faces, indicating an effect of expression and familiarity at the stage of structural encoding. The conclusion that structural encoding is influenced by both expression and familiarity is strengthened by the finding that N170 amplitude was larger for easy than for hard familiarity discriminations. In addition, famous faces elicited a larger P300 than did unfamiliar faces, as in our previous study (Martens et al., 2010), whereas familiarity difficulty exerted a stronger effect on P300 amplitude on no-go trials than on go trials, indicating that easy familiarity conditions were less resource demanding than were hard conditions (see Kok, 2001). By contrast, the earlier EPN deflection revealed a significant difficulty effect of

familiarity discrimination also on go trials, which might indicate that EPN reflects processes that are important in the analysis of facial identity, which is also consistent with the observed familiarity effect. Further implications of the ERP findings will be discussed in the General Discussion section.

The key findings of Experiment 2 concern the influence of facial familiarity discriminability on behavioral and electrophysiological measures of information processing. Responses were clearly faster when facial familiarity decisions were easy, rather than hard. In contrast to RT, the S-LRP interval was completely unaffected by familiarity difficulty, whereas the LRP-R interval was longer for hard than for easy familiarity discriminations. The latter finding indicates an effect on motor-processing time—that is, an extended interval from selective hand activation to response execution when facial identity processing is hard. The present LRP findings clearly contradict the parallel-contingent model with discrete output to response-related stages (Schweinberger et al., 1999). That is, due to the contingency between facial identity and expression processing, the S-LRP interval was predicted to reveal an effect of discrimination difficulty, which clearly was not observed. It is noteworthy that this observation also disagrees with the continuous version of the parallel-contingent model. We view it unlikely that the absence of an effect on the S-LRP interval is due merely to a lack of statistical power: In the context of an RT effect of more than 50 msec between the fastest and slowest condition combination (happy-easy vs. angry-hard), any “true” effect on the S-LRP should have produced at least a numerical trend. For comparison, in our previous study (Martens et al., 2010), we found, for a participant group of identical size (Experiment 2, $N = 16$), that the S-LRP interval indicated a statistically significant 29-msec familiarity effect. In the present study, it was the LRP-R interval that was prolonged by 21 msec for hard over easy familiarity decisions, indicating a motoric locus of the present RT difficulty effect. This finding is clearly inconsistent with the predictions made by the parallel-contingent model with

discrete output. Altogether, on the basis of present LRP findings, we rule out the parallel-contingent model as a viable account of face perception. This agrees with the conclusions we arrived at in our earlier study (Martens et al., 2010), in which, for different task demands, we found no support for this processing architecture either.

By contrast, the parallel model is fully consistent with the LRP findings in Experiment 2. Thus, the fact that the S–LRP interval was clearly uninfluenced by familiarity difficulty supports the view that information from expression analysis is directly transmitted to response-related processing stages. Moreover, the absence of the no-go LRP indicates that facial familiarity processing, even when hard to discriminate, was fairly similar in duration to expression processing. That is, the extended waiting time for the go/no-go decision for hard, as compared with easy, familiarity discriminations was not substantial enough to give rise to a no-go LRP. However, the LRP–R interval reflected this delay in facial identity processing over the duration of the expression analysis. Altogether, we assume that a parallel-processing model, in which facial familiarity is processed faster than expression under normal circumstances (i.e., easy discriminability), can explain the present LRP findings best.

GENERAL DISCUSSION

We investigated the temporal organization and functional architecture of facial familiarity and expression processing by using a hybrid two-choice go/no-go task, thereby overcoming the limitations of earlier studies that investigated both cognitive processes separately. In this task, decisions about response hand depended on facial expression information and the go/no-go decision on facial familiarity; that is, the S–R mapping was reversed, as compared with our earlier study, in which we established faster facial identity than expression analysis in a parallel-processing architecture (Martens et al., 2010). First, this allowed us to more specifically test whether the time course of facial identity and expression processing is subject to task-related effects, as induced by the higher probability of go than of no-go responses. Second, we also assessed whether processing of facial identity and expression has already bifurcated at the level of structural encoding by examining the N170 component and other visual ERP components.

Temporal Organization of Facial Familiarity and Expression Analysis

In both experiments, RT decreased with increasing number of repetitions of an individual face. Crucially, repetitions did not modulate the influence of facial expression (happy vs. angry) and the difficulty of go/no-go decisions on the time course of information processing. In addition, a comparable effect of repetitions was observed in RTs to famous and unfamiliar faces. These results suggest that repetitions led to a general speedup of information processing but did not selectively influence the processing of expression and facial identity analyses or their interaction under the conditions of the present study.¹

Most important, the LRP findings in Experiments 1 and 2 provided strong evidence for the assumption that facial identity and expression are processed in parallel, in line with the conclusions we arrived at in our earlier study (Martens et al., 2010). That is, in Experiment 1, the time interval from stimulus onset to the onset of the LRP increased for hard, as compared with easy, expression decisions, which is expected given that response hand and, hence, selective hand activation, as reflected by the LRP, depended on facial expression information. By contrast, in Experiment 2, the S–LRP interval was unaffected by the manipulation of familiarity difficulty, suggesting that activation of response hand was independent of facial familiarity processing, consistent with the parallel model (Bruce & Young, 1986), but not the parallel-contingent model, of face perception (Schweinberger et al., 1999). Further in line with the parallel model is the finding that the LRP–R interval was not influenced by experimental conditions in Experiment 1, whereas it was longer for hard than for easy familiarity discriminations in Experiment 2. Importantly, the latter finding disagrees with a variant of a parallel-contingent model that assumes discrete output from facial expression analysis to response-related processing stages, a model version that, in principle, would have been consistent with the LRP findings in Experiment 1. Finally, the absence of a no-go LRP in both experiments indicates faster processing of facial identity than of expression when both dimensions are easy to discriminate, with expression analysis gaining a slight temporal advantage over facial identity processing when familiarity decisions are hard, as indicated by the LRP–R interval effect in Experiment 2.

On the basis of present LRP findings, we rule out the possibility that the specific task demands of the hybrid two-choice go/no-go task induced strategic effects in such a way that, due to the higher probability of go than of no-go responses, participants prioritized the go dimension. That is, because, in our earlier study (Martens et al., 2010), activation of response hand depended on the familiarity decision, this could have led, in principle, to faster processing of facial identity than of expression. However, in the present study, the time course in processing these two facial dimensions was broadly replicated, despite using a reverse S–R mapping. Therefore, we conclude that strategic (top-down) effects do not change the temporal organization of facial identity and expression analyses. Rather, it appears that each component stage of the face recognition system responds quite selectively to the specific processing demands, thereby producing relative selective influences on the duration of facial identity and expression analyses.

However, one limitation of the present study needs mentioning, which concerns the fact that LRP onset measures were determined in jackknife-based waveforms that were obtained by averaging across facial familiarity. As a result, possible modulating influences of facial familiarity on expression processing could not be examined. For example, in our previous study (Martens et al., 2010), LRP measures indicated that expression information was much more readily available for famous face than for unfamiliar

iar face expressions, on the basis of which we proposed a parallel-dependent model of face perception. According to this model, identity and expression analysis of familiar and unfamiliar faces occurs in parallel, but expression processing of familiar faces relies on identity-dependent representations. Present chronometric LRP data do not allow us to address this issue. Thus, it is quite possible that expression-related LRP interval effects are of different magnitude for unfamiliar and famous faces.² For example, Wild-Wall, Dimigen, and Sommer (2008) found a shorter S-LRP interval for familiar, but not for unfamiliar, faces displaying a happy expression rather than disgust. Similarly, the RT data in Experiment 2 tentatively indicated a larger expression effect for famous than for unfamiliar faces. Also, present accuracy and N170 amplitude data (see the Expression Processing and Face Perception Models section) point toward identity-dependent expression analysis of famous faces, consistent with evidence indicating that facial representations are stored with preserved information of the facial expression with which the face is mainly experienced (e.g., Baudouin, Gilibert, Sansone, & Tiberghien, 2000; Kaufmann & Schweinberger, 2004). It is for future work, however, to more specifically examine the interaction of facial identity and expression processing in order to elaborate parallel-dependent face perception models.

Expression Processing and Face Perception Models

In contrast to some earlier studies (e.g., Eimer & Holmes, 2002; Williams et al., 2006), we failed to find an early expression effect on the anterior N120. However, studies demonstrating an N120 effect presented fearful rather than angry faces, which might explain the absence of early expression effects, as in other, similar ERP studies that did not show such effects on ERP waveforms before the N170 component (e.g., Ashley, Vuilleumier, & Swick, 2004; Batty & Taylor, 2003). Also, evidence for an early expression effect on sensory encoding appears inconclusive, because posterior P120 amplitude was reliably elevated for happy, as compared with angry, faces in Experiment 2, but not in Experiment 1. It is noteworthy, though, that this P120 amplitude effect is inconsistent with the view that negative facial expressions capture attention more efficiently than do happy faces (see Fox et al., 2000). That is, because the P100 component is known to increase with spatial attention allocated to a stimulus (e.g., Mangun & Hillyard, 1991), a larger, rather than a smaller, P120 should have been obtained for angry faces. Alternatively, it could be that the larger negativity for angry than for happy faces already starts in the P120 time range, thereby reducing the amplitude of this component.

Differences between the processing of happy and angry expressions were consistently observed in Experiments 1 and 2, starting in the time range of the N170 component. Thus, N170 amplitude was larger for angry than for happy faces and also was influenced by expression discriminability (expression intensity) in Experiment 1 and by the difficulty of familiarity decisions, as well as by familiarity, in Experiment 2. These findings clearly disagree with

previous studies that showed N170 amplitude to be unaffected by expression (e.g., Eimer & Holmes, 2002; Eimer, Holmes, & McGlone, 2003) but accords with and extends studies reporting expression effects on N170 amplitude for fearful, but not for neutral or happy, faces (e.g., Batty & Taylor, 2003; Leppänen et al., 2007; Williams et al., 2006) to task conditions of joint facial identity and expression analyses. Methodological differences in terms of task demands and stimulus material might account for the fact that two earlier studies failed to show larger N170 amplitudes for angry, as compared with happy, faces (Batty & Taylor, 2003; Schupp et al., 2004).

How can the present N170 effects be interpreted? In our view, at least three scenarios are possible for explaining the N170 findings. First, assuming that N170 reflects the structural encoding of faces, the present N170 results could indicate that facial identity and expression processing have not yet bifurcated at this stage. This inference contrasts with the assumptions of the parallel face perception model of Bruce and Young (1986), whereas it accords with the idea that facial identity codes and facial expression codes are extracted from a common representational system (see Calder & Young, 2005).

Second, following a proposal by Sprengelmeyer and Jentsch (2006), one might suggest that structural encoding entails two hierarchical subprocesses that initially involve viewpoint-dependent descriptions and subsequently expression-independent descriptions. According to this model, following the viewpoint-dependent description process, facial expressions are initially analyzed at a stage that codes emotional intensity and only subsequently by a system that derives expression-specific codes. However, such a hierarchical coding of expression seems unlikely for two reasons. First, we found the same ERP component (N170) to be influenced by both discrimination difficulty and facial expression. Second, Utama, Takemoto, Koike, and Nakamura (2009) reported an effect of facial expression on the P100 component and of expression intensity on the N170 component, indicating, if anything, the reverse temporal organization of expression and intensity coding. Since, to date, only a few studies have investigated the interplay of facial expression and intensity, producing inconsistent results, further research is needed.

Finally, and perhaps most likely, the present N170 amplitude effects may suggest that angry faces received more attention than did happy faces and, also, that the allocation of additional attentional resources to the encoding of familiar faces increases N170 amplitude, in line with similar proposals in the literature (see Eimer, 2000). This view, which is corroborated by recent research demonstrating strong sensitivity to selective attention of the N170 (Mohamed, Neumann, & Schweinberger, 2009), is attractive in the light of theoretical notions that automatic processing and/or an attentional bias is most likely triggered by negative facial expressions. Thus, faces displaying threat or danger may receive prioritized processing because, if such expressions are rapidly detected, it may confer a crucial survival advantage (e.g., Öhman, 2002; Vuilleumier, 2002). Accordingly, attention is captured by the highly socially relevant facial expressions. However, whether this

is indeed reflected by enhanced N170 amplitude for angry (and fearful) faces is up for debate and appears to be difficult to decide on the basis of the present findings.

In conclusion, and in line with earlier research (Caharel, Courtay, Bernard, Lalonde, & Reba, 2005; Martens et al., 2010), the data in the present study corroborate the assumption of parallel processing of facial identity and facial expression. A novel insight is that such processing occurs independently of the specific task demands and/or the strategic allocation of attention to specific facial dimensions. Furthermore, we replicated a temporal advantage for the analysis of happy faces and demonstrated the usefulness of the LRP for investigating the temporal organization of cognitive processes. The present N170 findings also suggest that a structural-encoding stage is common to both facial identity and facial expression perception (see also Calder & Jansen, 2005). For future research, it may be useful to appreciate that the process of structural encoding is far from being fully understood. As a perspective, a deeper understanding of structural face encoding may require considering different components (e.g., Calder et al., 2001) that code identity and expression to different degrees.

AUTHOR NOTE

The project was funded by a grant from the Biotechnology and Biological Sciences Research Council (BBSRC S20041), U.K., to S.R.S. and H.L. A portion of this research appeared in the dissertation of U.M. and was presented at the 45th Annual Meeting of the Society for Psychophysiological Research, September 2005, Lisbon, Portugal. Correspondence concerning this article should be addressed to U. Martens, Department for General Psychology, University of Osnabrück, FB 08/General Psychology I, Seminarstr. 20, 49074 Osnabrück, Germany (e-mail: umartens@uni-osnabrueck.de).

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NOTES

1. We thank an anonymous reviewer for making us aware of this problem and for suggesting the repetition analysis.
2. We thank an anonymous reviewer for raising this possibility.

(Manuscript received April 8, 2010;
revision accepted for publication July 16, 2010.)