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Holistic Processing of Faces: Learning Effects with Mooney Faces

Marianne Latinus and Margot J. Taylor*

Abstract

■ The specialness of faces is seen in the face inversion effect, which disrupts the configural, but not the analytic, processing of faces. Mooney faces, which are processed holistically, allowed us to determine the contribution of holistic processing to the face inversion effect. As inverted Mooney faces are difficult to recognize as faces, we also included an intermediary training period for Mooney face recognition for half of the subjects. Early face-sensitive ERPs (N170 and P1) and P2 were measured.

Behavioral data showed an increase in correct responses to inverted and upright Mooney faces after the learning phase for the experimental group. No effects were seen on P1. N170 latency did not vary with stimulus type before the interme-

diary phase, however, N170 amplitude was consistently larger for upright than inverted Mooney faces. After the intermediary exercise, N170 was delayed for inverted compared to upright Mooney faces. In contrast, for both groups of subjects P2 amplitude was larger for nonface stimuli, and P2 amplitude decreased after the intermediate task only for the subjects trained to recognize Mooney faces.

As the usual inversion effect seen with photographic faces (delayed and larger N170) was not seen with Mooney faces, these data suggest that this effect on N170 is due to the recruitment of analytic processing. P2 reflected learning and a deeper processing of the stimuli that were not identifiable as faces. ■

INTRODUCTION

Studies in several domains of the neurosciences have investigated the question of the specialness of face recognition, examining face versus nonface stimuli. Differences between face and object processing have been explained by various theoretical models. One model argues that differences occur at the level of recognition; that face and object detection depend on the level of expertise. A second model has suggested that differences between face and object processing could be explained by the existence of separable systems, each preferentially involved in processing one or the other category. These differences between face and nonface stimuli could also be due to the processing itself differing; the primary processing of faces may be configural and holistic and for objects analytical, which could also have the corollary of implicating separable structures.

According to the expertise model, faces and objects are processed by the same system but differences arise at the level of recognition. This theory proposes that face processing is different from object processing because faces are generally recognized at the subordinate (e.g., macaque) or identity (e.g., Suzy) level, whereas objects are recognized at the superordinate (e.g., ani-

mal) or basic (e.g., monkey) level. This was proposed by Diamond and Carey (1986) as they found an inversion effect for dogs only with dog experts. Expertise theory for faces is based on the importance of faces in our environment, and face expertise would be characteristic of humans. Gauthier, Skudlarski, Gore, and Anderson (2000) and Gauthier, Tarr, Anderson, Skudlarski, and Gore (1999) showed that objects recognized at the subordinate level can lead to similar responses as seen to faces. For example, in an fMRI study, bird experts recognizing birds at the subordinate level showed a similar activation in the fusiform gyrus as seen in face recognition tasks (Gauthier, Skudlarski, et al., 2000). Moreover, Gauthier, Tarr, et al. (1999) showed that only after acquiring expertise with novel objects was the fusiform gyrus activated.

Several lines of neuroscience research have suggested, however, that visual stimulus processing is modular depending on the category to which stimuli belong. Single-cell studies have provided evidence for this model by showing the existence of face specific cells in the inferotemporal cortex (IT) and superior temporal sulcus (Logothetis & Scheinberg, 1996; Perrett, Hietanen, Oram, & Benson, 1992). Intracranial event-related potential (ERP) studies in humans have shown activity specific to faces (the N200) in IT (Allison, Puce, Spencer, & McCarthy, 1999; Allison, McCarthy, Nobre, Puce, & Belger, 1994) with discrete localizations of N200 to

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faces adjacent to areas that appeared sensitive only to other categories (e.g., numbers or letter strings). Scalp ERPs also have demonstrated a face-sensitive activity over temporo-occipital sites, the N170 component (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bötzel, Schulze, & Stodieck, 1995). N170 is consistently larger to faces than to a range of nonface stimuli (Itier & Taylor, 2004; Itier, Latinus, & Taylor, 2003; Bentin, Alison, et al., 1996) and discriminates among face stimuli (Sagiv & Bentin, 2001; Taylor, Edmonds, McCarthy, & Allison, 2001; Bentin, Alison, et al., 1996; George, Evans, Fiori, Davidoff, & Renault, 1996). Functional imaging has also allowed visualization of brain regions that are involved specifically in face detection (e.g., Haxby, Ungerleider, Horwitz, et al., 1996; Sergent, Ohta, & MacDonald, 1992). Puce, Allison, Asgari, Gore, and McCarthy (1996) were the first to show with fMRI that faces preferentially activated regions of the fusiform gyrus, whereas adjacent areas in the inferior and occipito-temporal cortices were activated by nonface stimuli. Subsequent to this initial study, fMRI has been used extensively to examine differences in the localization of activation to face and non-face stimuli (Haxby, Ungerleider, Clark, et al., 1999; Kanwisher, Stanley, & Harris, 1999).

Finally, in the neuropsychological literature, there are a number of case studies with impairment in object (agnosia) (Moscovitch, Winocur, & Behrmann, 1997) or face (prosopagnosia) recognition (Michel, Poncet, & Signoret, 1989), which provide strong evidence of different neural networks involved in face and object processing. In particular, Moscovitch et al. (1997) studied a patient (CK) with visual agnosia associated with normal face recognition. They showed that CK had difficulties only in recognizing faces with configural disruptions, such as inverted faces. They suggested that two recognition systems were involved in visual stimulus detection. One system was involved in holistic processing, used by face detection. The other was involved in analytic processing (part-based processing), used in the recognition of objects and inverted faces.

Behavioral data have shown significant differences in processing upright and inverted faces; face recognition is poorer and reaction times are increased when faces are inverted, called the face inversion effect (Farah, Tanaka, & Drain, 1995; Rhodes, Brake, & Atkinson, 1993). Because inversion effects are much larger for faces than for objects (Yin, 1969), processing differences between upright and inverted faces have been investigated in efforts to understand the specialness of faces.

Face inversion effects are seen in neuroimaging studies, as the fusiform gyrus is less activated by inverted than upright faces (Kanwisher, Tong, & Nakayama, 1998) and face inversion increases the activation in object-selective regions (Haxby, Ungerleider, Horwitz, et al., 1999). Scalp ERP studies also provide neurophysiological evidence of the face inversion effect: N170 is larger and later for inverted faces (Bentin, Allison, et al.,

1996; Rossion, Gauthier, et al., 2000; Taylor et al., 2001). Evidence of the inversion effect on N170 suggests that N170 reflects combined sources, which result in differential activation with inversion of two systems implicated in face processing, holistic plus analytic (Sagiv & Bentin, 2001) consistent with the neuropsychological literature (Moscovitch et al., 1997).

Although many neurophysiological face processing studies have focused on N170, other ERP components (P1 and P2) have been analyzed in some studies to have a finer definition of the early processing of the visual stimuli. Rossion, Delvenne, et al. (1999) argued that P1 reflects low-level feature processing, as they did not observe any inversion effect on P1. However, Linkenkaer-Hansen et al. (1998) found differences between upright and inverted faces on P1 with stimuli that shared the same low-level features. Moreover, they showed no face inversion effect on P1 if the faces were degraded. Hence, they suggested that mechanisms underlying P1 were not sensitive enough to detect degraded faces. Face inversion effects on P1 have also been demonstrated from young children to adults (Taylor et al., 2001) and in adults with differing configural changes (Itier & Taylor, 2002; Halit, de Haan, & Johnson, 2000).

Several researchers have suggested that the predominant processing of upright faces is holistic (Moscovitch et al., 1997; Tanaka & Farah, 1993) with analytic or feature-based processing being involved with unusual face stimuli or objects. Configural processing (the relations among facial features within a face), however, is generally viewed as central to face processing. Maurer, Le Grand, and Mondloch (2002) suggested an initial configural processing stage that encodes the eyes above the nose, which is above the mouth; a second, holistic stage sees the face as a gestalt or whole; and a third, configural stage is the more classic configural processing of second-order relations (Rhodes, Brake, Taylor, & Tan, 1989; Diamond & Carey, 1986). The separation between the first two of these proposed stages is fine, as it is the perception of the facial features in the appropriate arrangement that gives the gestalt of a face. Faces are perceived more rapidly than objects (Purcell & Stewart, 1988), which relies on this early configural/holistic processing, whereas the second-order configural processing, which allows recognition of a specific face, occurs subsequently. Configural processing is particularly disrupted with inversion, whereas featural and holistic processing are not or less disrupted (e.g., Freire et al., 2000; Leder & Bruce, 2000). This difficulty of processing inverted faces is indexed behaviorally by poorer recognition and neurophysiologically by later and larger N170s. Consistent with this are the results of Sagiv and Bentin (2001) who found that inversion of schematic faces (smiley faces) that contain no identity information did not produce the usual N170 amplitude increase.

Mooney faces are black-and-white photographs of faces taken in a dark-contrasted environment leading

to incomplete representations of faces. They were first used to study closure ability and its development (Mooney, 1957), and have been used to assess holistic processing of faces (Moscovitch et al., 1997). Using Mooney faces where the first level of processing is holistic (as there are no separable features to be identified, as eyes over nose, above mouth) would allow us to better determine the contribution of holistic processing to facial recognition. Because of their incompleteness, analytical processing is not effective with Mooney faces; they require holistic processing to be categorized whether presented upright or inverted. Once recognized as faces, however, they could then be processed analytically, as the subject confirms the presence of a face. Kanwisher, Tong, et al. (1998) showed that accuracy for the detection of Mooney faces was inferior to the accuracy for the detection of regular faces, and that detection was particularly disrupted for inverted Mooney faces. They also found that inverted Mooney faces did not activate the same area on the fusiform gyrus as photographic faces, although it was activated by upright Mooney faces. Rotations of Mooney faces away from the vertical produced reduction both in perception of the faces and the amplitude of the face-sensitive vertex-positive peak measured frontocentrally (Jeffreys, 1993, 1996). The inversion effect of Mooney faces has not been studied with posterior-temporal ERPs, which would help separate holistic and analytic contributions to the early ERPs (P1, N170, P2), and provide temporal measures of these processes. This was one of the purposes of the present study; we wished to determine whether there were differences in the processing of upright and inverted Mooney faces; that is, if the Mooney face inversion effect is similar to the one found for photographic faces—delayed latencies and increased amplitudes of early face-sensitive components.

Moreover, as Mooney faces are much more difficult to see as faces when presented upside-down, we also trained our subjects in Mooney face recognition to see if training would have an impact on accuracy, and to see if increasing accuracy was correlated with neurophysiological changes. In order to separate repetition and learning effects, we performed a random division of subjects into two groups (experimental group and control group). The experimental group underwent an interactive training period on Mooney face recognition and the control group completed an unrelated visual categorization task. As repetition or learning could lead to the development of an expertise or improved face detection for these stimuli, we compared the ERPs before and after the learning/control task between upright and inverted Mooney faces to reveal neurophysiological correlates of learning.

Thus, the aims of the present study were to determine the contribution of holistic processing to face recognition and how this is reflected in face-sensitive ERPs.

Moreover, including a learning phase would provide information on the neurophysiological correlates of perceptual learning on early ERPs sensitive to faces.

RESULTS

Behavioral Data

Subjects performed a face/nonface detection task using Mooney faces presented upright and inverted, or scrambled Mooney faces (i.e., nonfaces; Figure 1). Subjects were grouped according to the intermediary exercise, and data were recorded before and after the learning/control task. Mean accuracy and reaction times as a function of stimulus type, group, and before/after the learning/control task were analyzed. Data were collapsed across groups before the learning/control task as statistical analyses showed no differences between the groups at this stage. Accuracy differed with stimulus type [$F(1,22) = 27.652, p < .001$]; upright Mooney faces and nonfaces were better identified than inverted Mooney faces. Training had an effect on accuracy as hits increased only for the experimental group, for both upright faces and inverted faces (Figure 2A). Reaction times (RTs) varied with stimulus type as upright faces were recognized faster than inverted faces (Figure 2B). RTs decreased after the learning/control task only for control group.

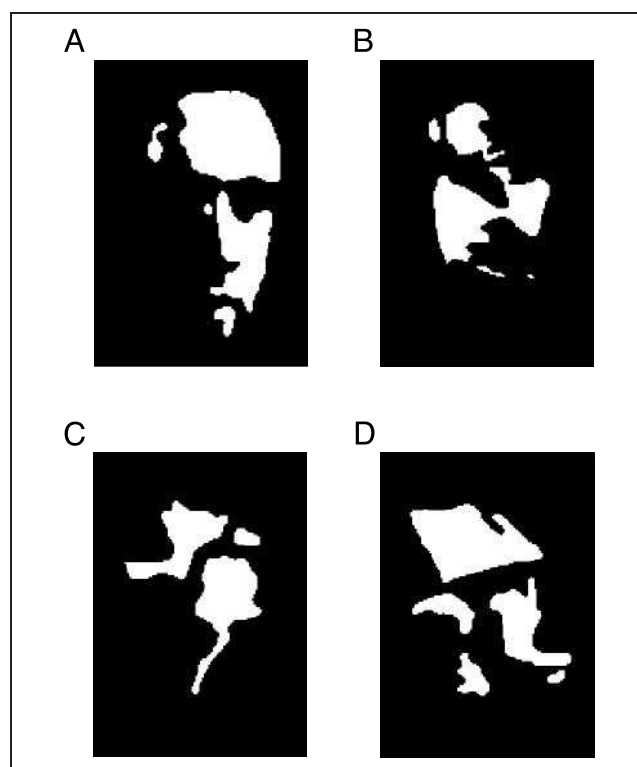
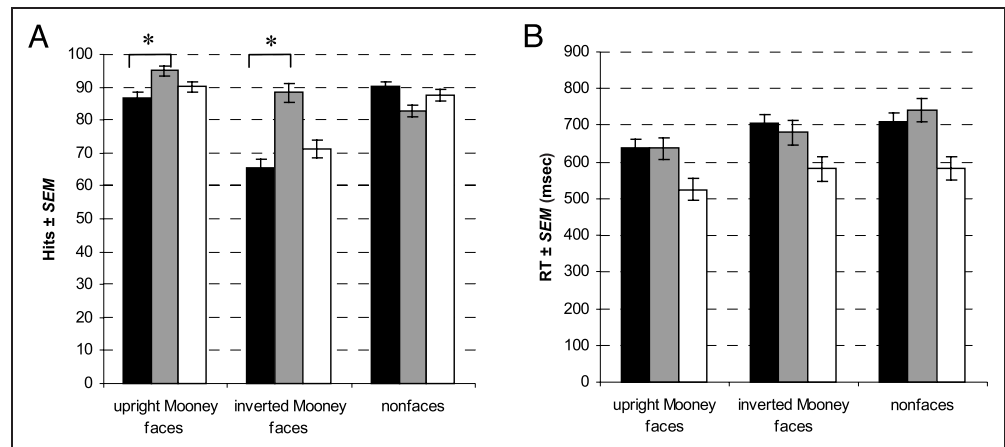


Figure 1. Examples of stimuli used. (A) Upright Mooney face; (B) Inverted Mooney face; (C, D) Nonfaces.

Figure 2. Mean accuracy and RTs as a function of stimulus type. (A) Accuracy; (B) RTs. Collapsed data for the two groups before the intermediary exercise (black bar). Data for the experimental group after the learning phase (gray bar). Data for the control group after the unrelated visual task (white bar). The hit rate for Mooney faces, upright and inverted, improved only for the group with learning. $*p = .001$



Electrophysiological Data

We measured the latencies and amplitudes of three visual ERP components over the parieto-occipito-temporal cortices (P1, N170, and P2; Figure 3).

P1

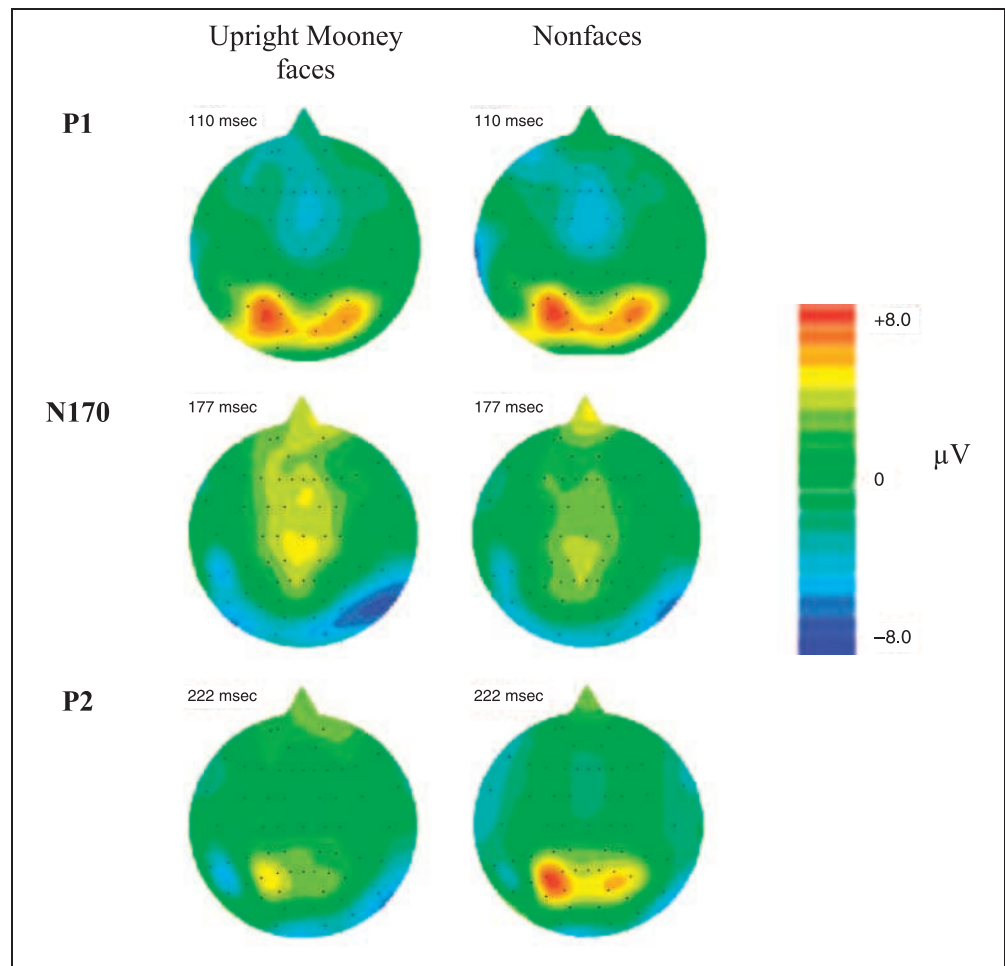
There was no effect of stimulus type on P1 latency or amplitude either before or after the learning/control

task, for either group of subjects. P1 was not affected by the inversion of Mooney faces.

N170

Before the learning/control task, N170 latency showed no effect of stimulus type. The learning/control task had no overall effect on N170 latency for either the experimental or the control group, regardless of stimulus.

Figure 3. Scalp distribution of the grand-averaged brain activity at the mean latency of each component for upright Mooney faces and nonfaces, using data of the experimental group before the learning phase.



However, as our interest was in the inversion effect, latency analyses comparing only upright and inverted Mooney faces were completed, which showed that N170 was delayed for inverted compared with upright Mooney faces only after the learning/control task [$F(1,22) = 6.97$, $p = .015$].

N170 amplitude differed among the stimulus types before the learning/control task; N170 was largest for upright Mooney faces, smallest for nonface stimuli, whereas inverted faces, perceived or not perceived as faces, were intermediate [$F(3,66) = 18.674$, $p < .001$] (Figure 4). There was a hemisphere effect on N170 amplitude [$F(1,22) = 7.37$, $p = .01$] due to upright Mooney faces evoking a larger N170 over the right hemisphere [Type \times Hemisphere: $F(3,66) = 4.09$, $p = .01$].

Comparisons between before and after the learning/control task showed the same pattern of effects of stimulus type on N170 amplitude [$F(2,44) = 61.13$, $p < .001$] as well as a lateralization of N170 only for upright Mooney faces [Type \times Hemisphere: $F(2,44) = 9.04$, $p = .001$]. After the learning/control task, N170 amplitude increased for both groups of subjects [$F(1,22) = 105.76$, $p < .001$] (Figure 5).

P2

No effects were seen on P2 latency. P2 amplitude varied according to stimulus type before the learning/control task [$F(3,66) = 27.03$, $p < .001$] (Figure 6) and in the before/after comparison [$F(2,44) = 68.12$, $p < .001$]. P2 was larger for nonfaces and inverted Mooney faces perceived as nonfaces than for upright and inverted Mooney faces correctly perceived.

Comparison between before and after the learning/control task showed a difference between groups; P2 amplitude decreased after the intermediate task only for

the experimental group [Training \times Group: $F(1,22) = 7.24$, $p = .013$] (Figure 7). As N170 effects could drive P2 effects, peak-to-peak analyses were conducted (P2 amplitude and latency minus N170 values); these analyses showed that the effects seen on P2 were independent of those seen on N170 as for both the amplitude and latency, the effects remained for P2 when only the N170–P2 differences were analyzed.

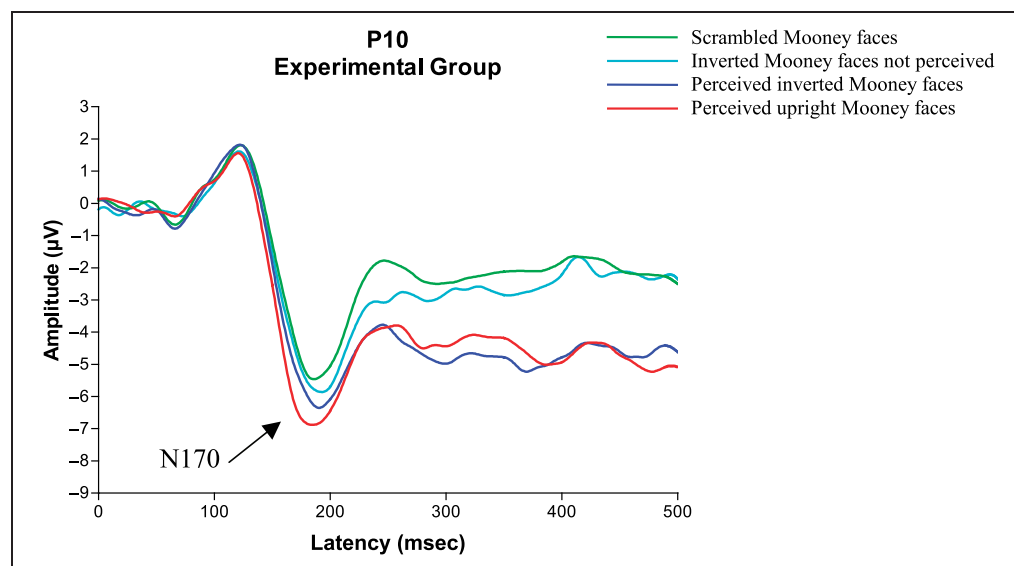
DISCUSSION

Our results showed a significant effect of training on accuracy in the experimental group; accuracy was improved only after the learning task. N170 amplitude was consistently larger for upright than for inverted Mooney faces, whereas N170 latency was delayed for inverted Mooney faces only after the learning/control task. P1 was unaffected by either stimulus characteristics or learning. Only P2 reflected learning; P2 amplitude decreased markedly for the experimental group after the learning task period. Whether before or after the learning/control task, P2 amplitude was largest for nonsense stimuli (i.e., nonfaces and inverted faces not perceived as faces) (Table 1).

Behavioral Data

We found that Mooney faces are less well perceived when inverted, consistent with other studies (Kanwisher, Tong, et al., 1998; George, Jemel, Fiori, & Renault, 1997; Jeffreys, 1993). Learning had an effect on accuracy, as increases in correct responses to upright and inverted Mooney faces were only seen after learning for the experimental group. However, differences between upright and inverted Mooney faces still remained after the learning period, comparable to the face inversion effect

Figure 4. N170 elicited by upright (red) and inverted (blue) Mooney faces perceived as faces, inverted Mooney faces not perceived as faces (turquoise), and nonfaces (green). Notice that N170 is largest for upright Mooney faces and smaller for nonfaces.



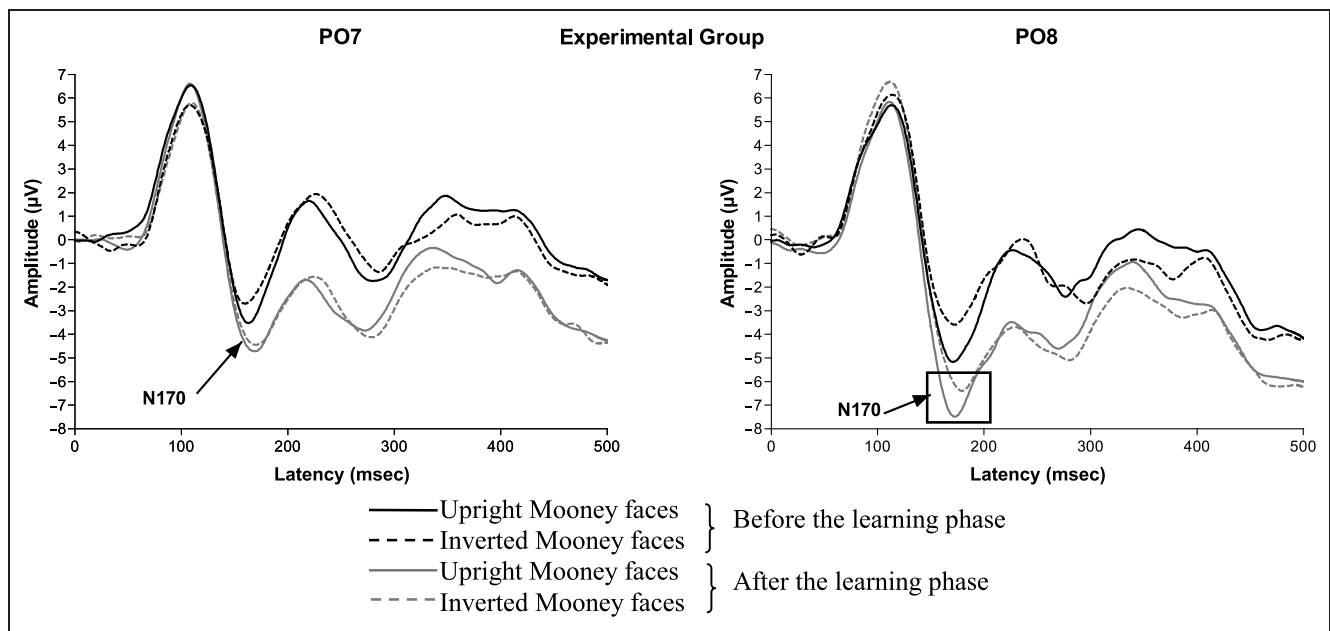


Figure 5. N170 elicited by upright (solid) and inverted (dotted) Mooney faces before the learning phase (black) and after the learning phase (gray) for the experimental group. Notice the smaller amplitude but delayed latency for inverted Mooney faces after the learning phase (in the square).

generally observed with photographic faces, due to the greater difficulty in recognizing inverted faces.

Subjects responded more rapidly for upright than for inverted Mooney faces, in accordance with results obtained with photographic faces (e.g., Itier & Taylor, 2002; Rhodes et al., 1993; Valentine, 1988). Somewhat surprisingly, learning had no effect on RTs in the experimental group, perhaps due to the difficulty of the task. RTs decreased, however, for the control group, explained by the control task requiring rapid responses to targets. The control group likely developed a pattern of responding quickly, whereas the experimental group learned to recognize Mooney faces without any emphasis on speeded responses.

Electrophysiological Data

P1

Our results showed no effects on P1 for face inversion or for face versus nonface stimuli as shown by some (Rossion, Delvenne, et al., 1999), although other studies have demonstrated that face inversion affects P1 amplitude and latency (Itier & Taylor, 2002, 2004; Taylor et al., 2001; Linkenkaer-Hansen et al., 1998). An explanation for the lack of P1 effects could be that Mooney faces may be considered degraded faces, as they are incomplete representations of faces. The first stage of configural processing proposed by Maurer et al. (2002) could not occur and the perception of a face would proceed from the second holistic stage of processing. Early neural mechanisms underlying P1, fine-tuned for face detection, may not be sufficient to process these faces adequately, as shown by Linkenkaer-Hansen et al.

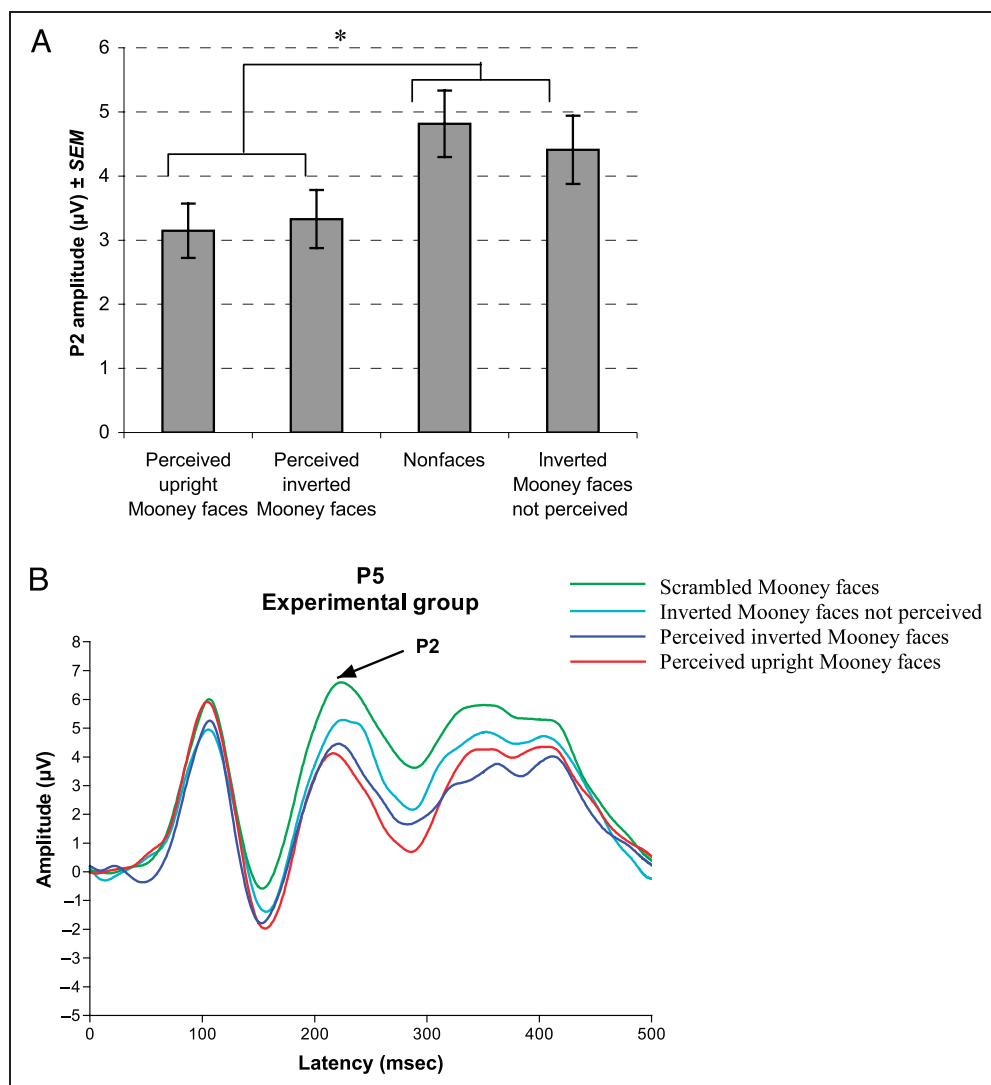
(1998), who found no effects of inversion on P1 with pointillized degraded faces. The inversion effect on P1 has been suggested to reflect early configural encoding of faces. Halit et al. (2000) demonstrated that configural disruptions other than inversion also led to variation in amplitude and latency of P1 in passive viewing face tasks. According to the above studies, an inversion effect would not be expected here on the P1, as the first stage of processing for Mooney faces is holistic rather than configural.

Some authors suggested that P1 may also reflect attentional modulations (Taylor, 2002; Halit et al., 2000). The above studies that used a passive viewing task (Taylor et al., 2001; Linkenkaer-Hansen et al., 1998) found P1 sensitive to inversion. Rossion, Delvenne, et al. (1999) used a priming recognition paradigm, during which subjects had to pay attention to faces and to second-order relations. Attention was directed to faces and required holistic processing and they showed no effect of inversion on P1. In a similar vein, Batty and Taylor (2003) found P1 effects in an implicit face processing task, but not in an explicit version using the same stimuli (Batty, Delaux, & Taylor, 2003). It appears that some P1 inversion effects are task-dependent. The present task required only detection, not recognition of faces, which may contribute to the lack of inversion effects on P1.

N170

N170 latency did not vary with face type before the learning/control tasks, however, N170 was larger for upright faces than for inverted faces and nonfaces.

Figure 6. P2 amplitude for all stimulus types before the intermediary exercise. (A) Collapsed data of the two groups of subjects ($*p \leq .002$). (B) Grand-averaged ERP waveforms for all stimulus types for the experimental group at the left parietal electrodes. Upright (red) and inverted (blue) Mooney faces perceived as faces, inverted Mooney faces not perceived as faces (turquoise), and nonfaces (green).



Hence, although inverting Mooney faces had an effect on N170, this effect differed from the one usually described for photographic faces: longer-latency and larger-amplitude N170s for inverted photographic faces (Taylor et al., 2001; Rossion, Gauthier, et al., 2000; Bentin, Alison, et al., 1996). Mooney faces are two-tone faces difficult to process either upright or inverted because of the incomplete internal features, thus they engage primarily holistic processing. Photographic faces, on the other hand, engage primarily second-order configural processing as they convey physiognomic information carried by the relation among internal features of the face, which provide identity information. Thus, inversion effect differences between Mooney and photographic faces are likely due to the recruitment of different levels of face processing. Consistent with this hypothesis are the results of Sagiv and Bentin (2001) that showed a delayed but smaller N170 inversion effect for schematic faces. They suggested that this finding was attributable to the involvement of different processes for inverted schematic compared to photographic faces. As

schematic faces did not carry physiognomic information, inverting them did not involve analytic processing, which is recruited for identification of inverted photographic faces. These results provide evidence for a sensitivity of N170 to the several types of processing invoked by faces. Photographic faces engage configural processing when presented upright, plus analytic processing when presented inverted. Upright Mooney faces engage holistic processing, as analytic processing is not effective and most probably not engaged, so there is no N170 amplitude increase when they are presented inverted. The N170 decrease in amplitude with inversion of Mooney faces could be due to the difficulty in engaging even holistic processing when these stimuli are inverted.

The nonface stimuli evoked a smaller negative potential than faces at the N170 latency. Usually, scrambled faces evoke little or no negativity (Taylor et al., 2001; Bentin, Alison, et al., 1996). The negative potential observed for nonface stimuli could be explained by contextual priming. Subjects were searching for faces

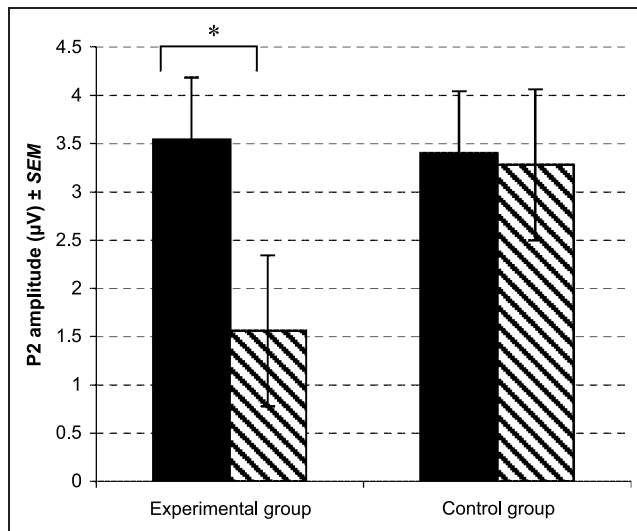


Figure 7. P2 amplitude for the two groups of subjects, across stimuli, before (solid) and after (dashed) the intermediary exercise. * $p < .05$.

and the nonfaces could elicit an N170 as they were examined as possible faces in this face detection context. This is in accordance with Bentin, Sagiv, et al. (2002), who have shown an N170 for schematic nonfaces (schematic eyes) once the context of faces had been established. Inverted faces not perceived as faces evoked a similar N170 as seen with inverted faces perceived as faces. This suggests that N170 in this context of a difficult face detection task reflects top-down modulation of perceptual processing for faces, even if a face is not always perceived.

However, after the learning/control task, there was an inversion effect on N170 latency as inverted Mooney faces evoked a longer-latency N170, although amplitudes were still larger for upright than for inverted Mooney faces. This latency effect could be due to repetition of the stimuli as it was observed for both groups of subjects. Repetition could involve a modification of Mooney face perception, such that subjects would try to process inverted Mooney faces analytically; the fact that no amplitude effects were seen suggests that this was not successful. Alternatively, the latency effect with inversion could be explained by the development of an expertise in Mooney face recognition. According to Gauthier, Skudlarski, et al. (2000) and Gauthier, Tarr, et al. (1999) expertise accounts for the inversion effect, although expertise would have had to result from the repetition of stimuli for only 40 min. In the study by Gauthier, Skudlarski, et al., the training that led to expertise lasted 7 hours a day for 4 days. The present experiment was likely too short to develop expertise, except that the participants were already face experts and they only had to learn to engage face processing during the learning phase for Mooney faces. Consequently, the repetition necessary for a change in the level of expertise would be shorter for these stimuli.

Our results also showed an increase in N170 amplitude after the intermediary exercise for upright and inverted Mooney faces. This is consistent with Tanaka and Curran (2001), who found larger-amplitude N170s to stimuli within subjects' domains of expertise. We would also suggest that with expertise, subjects build a recognition pattern for stimuli within the domain of expertise. The inversion of such stimuli, however, even

Table 1. Mean Latencies and Amplitudes for the Three Components by Condition

	<i>Before the Learning Phase</i>				<i>After the Learning/Test Phase</i>		
	<i>Upright Mooney Faces</i>	<i>Inverted Mooney Faces</i>	<i>Not Perceived</i>	<i>Nonfaces</i>	<i>Upright Mooney Faces</i>	<i>Inverted Mooney Faces</i>	<i>Nonfaces</i>
<i>P1</i>							
Latency (msec)	107.60	108.37	108.38	107.03	108.22	107.72	107.34
Amplitude (µV)	4.92	5.12	4.97	5.15	5.14	5.28	5.37
<i>N170</i>							
Latency (msec)	176.82	177.47	176.81	177.74	177.44	179.79	179.27
Amplitude (µV)	-4.92	-4.15	-3.54	-3.20	-6.82	-5.93	-5.04
<i>P2</i>							
Latency (msec)	221.79	221.80	221.95	223.36	218.69	219.64	220.89
Amplitude (µV)	3.15	3.33	4.41	4.82	1.86	2.01	3.39

Note the amplitude increase for N170 after the learning phase but the decrease for P2 (in **bold face**).

if only recently acquired, could disturb the usual perception and interfere with the automatic activation of the recognition processes related to the expertise. George, Jemel, et al. (1997) also showed an increase of N170 amplitude with Mooney face repetition, and suggested that this increase reflected a facilitation of perception. In contrast, repetition effects with photographic faces show an N170 amplitude decrease (Itier & Taylor, 2002), further demonstrating that Mooney faces and photographic faces are not processed the same way, although both types of faces show greater right-sided amplitudes, unlike nonface stimuli. There was no differential effect of the intermediate task on the N170 amplitudes for the two groups of subjects. Learning did not seem to have a neurophysiological correlate at these early stages of processing, despite its large effect on behavior. Nonetheless, we would speculate that although the present learning was not sufficient to induce changes in P1 or N170, a longer learning might produce such effects.

The combination of the above results suggests that upright photographic faces are processed holistically and configurally and, when presented inverted, they further recruit analytic processing, associated with processing nonface objects (Haxby, Ungerleider, Clark, et al., 1999). Analytical processes implicated in face processing may well be distinct from the routine object-related analytical processes, as they appear to be recruited for feature-based face analyses in the circumstances of attempting recognition under unusual conditions such as inversion. We would suggest that becoming an expert leads to the construction of patterns of recognition, such that stimuli previously processed analytically or by features would come to be processed automatically (i.e., holistically). Inversion produces recognition disruption due to discordance between typical and inverted stimuli, thus analytic processing would be invoked (when it is permitted by characteristics of the stimulus) for identity-level access. With Mooney faces this was not feasible, as they require primarily holistic processing, leading to the lack of amplitude effects when they are presented inverted.

P2

Although less frequently measured than P1 and N170, P2 showed very interesting and task-specific effects in the current study. P2 amplitude varied with stimulus type before and after the learning/control task, being larger for nonfaces and inverted Mooney faces not perceived as faces, than for upright and inverted Mooney faces correctly identified. This suggests that neuronal mechanisms underlying P2 might be involved in deeper or more extensive processing of stimuli not yet identified. Although P2 was not analyzed in the article of Sagiv and Bentin (2001), the P2 seen in Figure 1 was larger for scrambled faces than for faces or flowers, consistent

with our results. After the learning period, we found P2 amplitude decreased only for the experimental group. This amplitude decrease linked to accuracy suggests that P2 may reflect a neurophysiological correlate of learning. Consistent with this reasoning, learning would lead to a certainty of perception, such that deep processing indexed by P2 was not as necessary.

Conclusions

Our results show that the learning effects seen behaviorally were not correlated with changes in neuronal activity reflected in the early face-sensitive ERP components (N170 and P1). The intermediary exercise had an effect on the latency and amplitude of N170 but this was not only due to learning. However, training decreased P2 amplitude; this would suggest that the learning period led to increased certainty of perception, which in turn led to decreased need for the in-depth stage of processing reflected by P2. Our data argue that the latency and amplitude effects seen on N170 with photographic face inversion are due primarily to the activation of feature-based analytic processing. The present lack of comparable inversion effects on Mooney faces is due to their recruiting primarily holistic processing.

METHODS

Subjects

Twenty-six adults (13 women) participated in the study (mean age: 23.9 years); all but one were right handed; the left-handed subject showed a very similar pattern of ERPs, so data were collapsed. All subjects reported normal or corrected-to-normal vision and reported taking no medication and had no history of neurological, ophthalmologic, or systemic disease. They gave informed written consent. The experiment was approved by the French Comité Opérationnel pour l'Ethique dans les Sciences de la Vie du CNRS.

The subjects were placed into one of two groups in a pseudorandom fashion ($n = 13$ in each). The first, experimental group (7 women), had a learning period for Mooney faces recognition; the second, control group (6 women), performed an unrelated visual task.

Stimuli

There were 320 stimuli, 80 in each of four categories: upright and inverted Mooney faces, and upright and inverted nonfaces (see Figure 1). Forty of the Mooney faces were those used by Craig Mooney (1957) in his classic study. The 40 new Mooney faces were created at our laboratory using *Web Cam Go* software to take photographs in a dark room with a high luminosity directed to the face of the person; it created shadows on the face. The brightness of the photograph was then

modified using *Image J* freeware; pixels were divided into pixels either with high or low brightness which led to black-and-white, high-contrast pictures. Inverted Mooney faces were a vertical symmetry of upright Mooney faces. Nonfaces were a scrambled form of the pixels of upright Mooney faces: Black-and-white patches of the images were moved to create nonsense stimuli; inverted nonfaces stimuli were a vertical symmetry of the upright nonfaces.

Experimental Procedure

Subjects were seated in a comfortable chair in a dark room. Stimuli were presented centrally on a screen 60 cm in front of the subjects. The stimuli subtended $10^\circ \times 11^\circ$; they were presented in a random order using *Presentation 6.0* for 300 msec with an ISI between 1200 and 1600 msec. Subjects pressed a keyboard key for faces with one hand and another key for nonfaces with the other hand. The hand used to respond to faces was counterbalanced across subjects. Four blocks of 80 stimuli (20 of each category) in random order were presented, followed by the learning/control task, and finally by a repetition of the four blocks. Presentation order of blocks was randomized across subjects and across before/after the learning/control task. Short breaks were given to subjects between blocks.

The learning phase consisted of the presentation of 20 Mooney faces shown upright and inverted, which were different from those faces used in the experiment. Subjects had time to examine the stimuli and to try to see the faces. The experimenter knew the stimuli well, could see all the Mooney faces, and thus could distinguish separable features, helped the subjects perceive the faces by “showing” them the features of the faces when necessary. The control task was a categorization task; subjects were presented with a series of 300 stimuli, 150 of which included animals, to which they were to respond as quickly and accurately as possible.

Data Recordings and Analysis

Behavioral performances, hits, and RTs were recorded using *Presentation 6.0*.

Electrophysiological data were recorded using 64 electrodes in a cap (*Easy Cap*), including three ocular sites to record eye movements. The electrodes were placed according to the 10/10 system. FCz was the reference during acquisition; an average reference was calculated off-line. Impedances were kept under 5 k Ω . EEG was recorded using *Neuroscan 4.2*, the signal was amplified using *Synamps* system (gain: 500). Data were recorded with a frequency of 1000 Hz through a band-pass of 0.1–100 Hz. Continuous EEG was epoched into 800-msec sweeps (including a 100-msec prestimulus baseline), baseline corrected and trials with ocular artifact between –100 and 400 msec >100 μ V were rejected. Epochs

were then averaged digitally as a function of stimulus category and correct or incorrect responses, and filtered at 0.1–30 Hz.

Peak analyses were completed on data recorded from each subject. Only averages of more than 15 artifact-free epochs were kept for analysis, such that only upright Mooney faces identified as faces, inverted Mooney faces identified as faces or not (only before the learning/control task), and nonfaces correctly classified as non-face stimuli were analyzed. Peak latency and amplitude were measured for three early components: P1 (maximal around 110 msec, 90–140 msec), N170 (maximal around 175 msec, 140–210 msec), and P2 (maximal around 220 msec, 180–260 msec). Components were measured at the electrodes where they were maximal over each hemisphere in the grand averages, and at the electrodes within the distribution of the component (see Figure 3 for the distribution of the activity for the three components). P1 was measured at parieto-occipital sites (P7, P8, P5, P6, P3, P4, P1, P2, PO7, PO8, PO3, PO4, O1, and O2), N170 at temporo-parieto-occipital sites (P9, P10, P7, P8, PO9, PO7, PO10, PO8, O9, O10, O1, and O2), and P2 at parieto-occipital sites (P5, P6, P3, P4, P1, P2, PO7, PO8, PO3, PO4, O1, and O2). For each subject and category, the peak was measured within ± 30 msec of the peak latency of the grand average. Latencies over each hemisphere were taken where peak amplitude was maximal (Picton et al., 2000).

Repeated-measures ANOVAs using SPSS were performed on individual data, *p* values reported here are those obtained after Greenhouse–Geisser correction. Intersubject factor was group. Intrasubject factors, before the learning/control task, were stimulus type (4 levels), hemisphere (2 levels), and for amplitude, electrodes (7 levels for P1 and 6 levels for N170 and P2). Before/after the learning/control task comparisons were done only for correctly perceived stimuli [stimulus type (3 levels)]; intrasubject factors then also included training (2 levels).

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