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Face to face: Blocking facial mimicry can selectively impair recognition of emotional expressions

Lindsay M. Oberman, Piotr Winkielman, and Vilayanur S. Ramachandran
University of California San Diego, La Jolla, California, USA

People spontaneously mimic a variety of behaviors, including emotional facial expressions. Embodied cognition theories suggest that mimicry reflects internal simulation of perceived emotion in order to facilitate its understanding. If so, blocking facial mimicry should impair recognition of expressions, especially of emotions that are simulated using facial musculature. The current research tested this hypothesis using four expressions (happy, disgust, fear, and sad) and two mimicry-interfering manipulations (1) biting on a pen and (2) chewing gum, as well as two control conditions. Experiment 1 used electromyography over cheek, mouth, and nose regions. The bite manipulation consistently activated assessed muscles, whereas the chew manipulation activated muscles only intermittently. Further, expressing happiness generated most facial action. Experiment 2 found that the bite manipulation interfered most with recognition of happiness. These findings suggest that facial mimicry differentially contributes to recognition of specific facial expressions, thus allowing for more refined predictions from embodied cognition theories.

In 1890, James observed that “Every representation of a movement awakens in some degree the actual movement which is its object.” Since then, a large number of behavioral studies found that observers tend to overtly and covertly mimic behavior of those around them (Condon & Ogston, 1967; Kendon, 1970). Specifically, people tend to mimic others’ gestures and body postures (Chartrand & Bargh, 1999), facial expressions (Dimberg, 1982; Dimberg, Thunberg, & Elmehed, 2000; Wallbott, 1991), tone of voice and pronunciation patterns (Goldinger, 1998; Neumann & Strack, 2000), and even breathing rates (McFarland, 2001; Paccalin & Jeannerod, 2000).

Early explanations of mimicry saw it as a simple by-product of previously established S–R links between perceiving and performing an action (Lipps, 1907). Contemporary research, however, provides evidence that in addition to action observation eliciting concurrent performance of that same action, the performance of an action influences the concurrent perception of that action. Specifically, concurrent performance of a compatible action tends to facilitate recognition whereas performance of incompatible actions tends to interfere with it (Reed & Farah, 1995; Tucker & Ellis, 1998). The findings that action execution and action observation reciprocally modulate each other suggest that mimicry occurs because action observation and action execution share a common representational code (Prinz & Hommel, 2002) and neural substrates (Grezes & Decety, 2001). More generally, the grounding of perceptual and conceptual understanding in the mechanisms underlying action in the world is the central tenet of embodied cognition theories (Niedenthal, Barsalou, Winkielman, Ric, & Krauth Gruber, 2005).

One of the most studied examples of the interaction between action observation and

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Correspondence should be addressed to: Lindsay M. Oberman, 9500 Gilman Drive, La Jolla, CA 92093–0109, USA. E-mail: loberman@ucsd.edu

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action execution is mimicry of emotional facial expressions. Facial mimicry has been explained in two ways. Some researchers propose that mimicry reflects the process of emotional contagion (Hatfield, Cacioppo, & Rapson, 1994; Laird et al., 1994). That is, observation of other's emotional expressions first triggers the corresponding emotion in the observer which then elicits the same facial expression (Lundqvist & Dimberg, 1995). However, some researchers propose that facial mimicry reflects an internal simulation of the perceived facial expression in order to facilitate understanding of others' emotion (Atkinson & Adolphs, 2005; Niedenthal, Brauer, Halberstadt, & Innes-Ker, 2001; Wallbott, 1991). There are now several models explaining how ''embodied simulation'' could help in emotion perception and understanding (see Goldman & Sripada, 2005, for a review). The assumption underlying those models is that the internal re-enactment provides useful information either through generation of peripheral feedback (e.g., facial muscles) or engagement of an ''as–if'' loop in the somatosensory and motor cortices (e.g., face representation). In short, resonating with the topic in this special issue, mimicry allows us to increase our ''interpersonal sensitivity'' through ''entering others' worlds.''

Recently, Niedenthal and colleagues (2001) provided behavioral evidence for the role of facial mimicry in perception of emotional facial expressions. Participants were asked to identify the point at which a morphed face changed from happy to sad and vice versa. During this task, some participants could freely move their facial muscles, but other participants were prevented from doing so by a pen held sideways in their mouth. Compared to the free movement condition, participants in the pen condition detected the change in expression later in both directions, thus supporting the role of facial mimicry in recognition of facial expressions. However, this study leaves several questions open. It is unclear whether blocking mimicry impairs recognition of any facial expression or is restricted to select expressions (happy, sad, both?). This is interesting as concurrent performance of facial movements may be more critical for recognition of some expressions rather than others, as we discuss shortly. Further, it is unclear whether mimicry is only important for detecting a dynamic transition between two different expressions, or also is involved in perception of single facial expressions. Finally, we know little about what specific muscles are influenced by the various manipulations, and whether these muscles are involved in the actual generation of facial expressions. These questions, addressed in our current work, are important for a more precise understanding of the role of somatosensory and motor resources in emotion perception.

Neural substrates of recognition

Embodied theories of cognition and emotion date back to philosophers Lotze (1852) and James (1890) and have also been occasionally proposed in psychology (e.g., Zajonc & Markus, 1984). However, the recent revival of such theories has been inspired by several recent developments in neuroscience. One is the discovery of mirror neurons. While studying the premotor cortex in the macaque, Rizzolatti and colleagues came across a system of neurons in area F5 that responded not only when the monkey performed an action, but also when the monkey watched the researcher perform a similar action (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). The team named this system of neurons the ''mirror neuron system'' (MNS) because it appeared that the observed action was reflected or internally simulated within the monkey's own motor system. Later studies by this same group further characterized this system as being selective for animate actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and is somatotopically distributed based on the effectors used to perform the action (Buccino et al., 2001; Goldenberg & Karnath, 2006). In general, the MNS is assumed to form an important mechanism of shared representation (Decety & Sommerville, 2003; Oberman & Ramachandran, 2007). There is also some specific evidence for activation in the human equivalent of the mirror neuron area (Brodmann area 44, in the premotor cortex) when participants imitate other people's facial expressions (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003).

A related discovery contributing to the resurgence of interest in the embodied theories of cognition is the observation that motor and somatosensory areas are involved in what has been assumed to be purely perceptual tasks, such as stimulus recognition. In the area of recognition of emotional facial expression, the contribution of somatosensory cortices was examined in a pivotal study by Adolphs and colleagues (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000). In that study, 108 focal brain lesion patients and 30 normal control participants were asked to perform three visual emotion recognition tasks. In the first task, participants were asked to rate the intensity of basic emotional facial expressions. In the second task, participants were asked to match a facial expression with the name of the emotion it was meant to convey. The final task required participants to sort facial expressions into emotional categories. Though each task identified a slightly different group of regions, damage to right somatosensory-related cortices impaired performance in all of the three tasks. Interestingly, the study did not find any differential effects of right somatosensory damage across expression type, but this could be because the study assessed damage to fairly broad regions that possibly support a variety of simulation mechanisms, including re-enactment of facial, postural, and visceral aspects of emotional experience.

Current studies

Interestingly, to this date, only few psychological and neuroscientific studies have examined the specificity of the embodied systems in recognition of emotion and action. For example, the behavioral studies using manipulations that block mimicry did not assess which specific muscles were influenced and to what extent, and how this involvement related to recognition deficits for specific expressions (Niedenthal et al., 2001). Even the neuroscience studies investigating the somatotopic specificity of mirror neurons have worked on a fairly gross level (e.g., leg, hand, face in Buccino et al., 2001, or hand and finger in Goldenberg & Karnath, 2006).

However, if embodied simulation indeed plays a critical role in recognition of facial expressions, then one should be able to formulate more focused hypotheses. One prediction is that blocking the ability to engage in facial mimicry should differentially impair recognition of different emotions from the face. Note that, most generally, different emotions engage different peripheral and central mechanisms, with specific engagement varying across stimuli and contexts (Barrett, Mesquita, Ochsner, & Gross, 2007). More specifically, emotions differ in the degree to which they are expressed in the face (Ekman, 2004). For example, happiness is associated with distinct changes in many facial regions. As a result, its simulation might be more ''external'' and predominately draw on the perceiver's own facial musculature. In contrast, sadness is associated with more subtle and localized facial changes. As a result, its simulation might involve more ''internal'' experience. Based on these considerations, we predicted that interfering with a simulation using facial muscles by creating irrelevant activation (muscular noise) should be most detrimental to recognition of expressions that involve most facial action, such as happiness, but have little effect on recognition of emotions that involve less facial actions, such as sadness.

To examine these questions, our main study, reported in Experiment 2, investigated whether experimental manipulations that block mimicry differentially impair recognition of specific facial expressions. However, in order to answer our central question, we first needed to better understand the effects of our manipulations and stimuli on facial muscles. Thus, we conducted Experiment 1 using electromyography (EMG) and tested (1) what muscles and to what extent are influenced by mimicry-blocking manipulations, and (2) what muscles and to what extent are involved in production of specific facial expressions. The results of this study allowed us to make more focused predictions for Experiment 2.

EXPERIMENT 1

We employed two manipulations that required participants to activate facial muscles in a task-irrelevant fashion and thus should interfere with mimicry. Our primary manipulation involved constant activation from having to bite on a pen with the teeth while not allowing it to touch the lips. The inspiration for this manipulation came from Niedenthal et al. (2001). However, in order to ensure muscle activation, we required participants to exert a constant active pressure on the pen whereas Niedenthal's manipulation required no muscular activity to keep the pen in the mouth. In other words, our manipulation creates an irrelevant muscular ''noise'' whereas Niedenthal's manipulation prevents generation of muscular ''signal.''[1]

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[1] Readers familiar with social psychology literature should note the difference between the above methods from manipulations aimed at temporarily inducing a specific emotional expression for the purpose of changing mood. Thus, Strack, Martin, and Stepper (1988) used a pen placed in a mouth like a writing instrument to induce a temporary increase in mood (when held in teeth and causing a light smile) and a decrease in mood (when held in lips so that it causes an expression of sadness). Note also that in our lip manipulation, the pen rests on the lips horizontally, not forming any particular expression.

Our second manipulation involved strong and cyclical activation of muscles around the mouth and jaw by a chewing action. This manipulation was adopted from a study that found that chewing gum while viewing neutral facial expressions might impair participants' performance at the later memory test for those expressions (Pietromonaco, Zajonc, & Bargh, 1981). Though this study dealt with neutral, rather than emotional facial expressions, and tested for a delayed memory for identity, rather than immediate discrimination of emotion type, we found it interesting to examine the gum manipulation as it potentially offers a powerful and widespread way of influencing mimicry (Zajonc & Markus, 1984).

We also included a control condition where participants held a pen horizontally with the lips while not allowing it to touch the teeth (''lip''). This action does not activate any mouth muscles and does not prevent mimicry and was included for the purpose of controlling for any possible effects due to performance of a concurrent task.

In addition to testing effects of mimicry-blocking manipulations on activity of specific facial muscles, we also tested which facial muscles are activated when performing facial expressions. Specifically, participants were asked to produce expressions of happiness, sad, fear, and disgust using either a model face presented on a computer screen, or on their own, in response to a verbal cue. Although many previous EMG studies examined the effects of making facial expressions (Tassinary & Cacioppo, 2000), we wanted to directly compare the degree to which each expression activated specific facial muscles, relative to the effects of external face manipulations.

Method

Participants

Participants were six individuals (4 male, 2 female) recruited through the psychology department at UCSD and ranged in age from 21 to 44 years ($M = 29$, $SD = 8.5$). Subjects volunteered their time and gave informed consent for the study.

Design and procedure

The study represented a within-subject design, with the presentation order of the conditions randomized. Following attachment of the electrodes, participants were asked to perform several tasks. The tasks fell into two groups designed to assess muscular effects of (1) external face manipulations and (2) expressions manipulations.

External manipulations. Participants were asked to (1) place a pen in their mouth horizontally and hold on to it using their teeth while not allowing their lips to touch the pen (''bite''); (2) chew gum (''gum''); and (3) place a pen in their mouth horizontally and hold onto it using their lips while not allowing their teeth to touch the pen (''lip'').

Expression manipulations. Participants were asked to voluntarily produce facial expressions of happiness, sadness, fear, and disgust by (1) imitating the expressions of a model presented on a computer screen, and (2) in response to a verbal cue, without a model.

Finally, we had a neutral ''rest'' condition where participants were asked to sit and relax their face for 10 seconds. This condition served as a baseline control.

Stimulus presentation

During the external face manipulation conditions, participants were verbally instructed to perform the requested action (chew, bite, lip). During the conditions where the participant was asked to imitate the model, stimuli were presented on a 15-inch monitor located approximately 80 cm away from the participant. Pictures were approximately 10 × 10 cm in size and came from the ''Pictures of Facial Affect'' set (Ekman & Friesen, 1976). During the expression-generation condition, participants were verbally instructed to make a relevant face (happy, fear, sad, and disgust).

EMG measurement and equipment

EMG was used to assess activity of muscles involved in generating facial expressions of happiness, disgust, fear, and sadness. Specifically, we monitored activity in the cheek region by recording from the zygomaticus major (muscle that raises the lip corner) and buccinator (muscle that retracts the lip corner). Based on previous work, we expected zygomaticus to be particularly activated by the expressions of happiness (Tassinary & Cacioppo, 2000). Previous work has also associated buccinator with smiles, especially posed or "fake" smiles likely to be generated upon request to make an expression (Ekman & Friesen, 1982). We also monitored the nose region (levator) as it has been implicated in the expressions of disgust (Vrana, 1993). Finally, we monitored activity in the lip region by recording from orbicularis oris—a perioral muscle responsible for a variety of mouth movements, including the widening sometimes seen in fear (Ekman, 2004). We did not expect any specific muscle activation for sadness as this emotion is generally associated with overall reduction in muscle tone.

Muscle activity was measured with pairs of adjacent silver/silver-chloride electrodes placed on the left side of the participant's face. An additional ground electrode was placed in the upper portion of the forehead. The impedances of all electrodes were reduced to less than 10 kΩ. The location of the electrodes and recording technique conformed to the standards for EMG recording (Cacioppo, Tassinary, & Fridlund, 1990). The acquisition of EMG signals was controlled by MP 150 Amplifiers and Acknowledge software package by Biopac Corporation. The signals were amplified by 2000 and filtered on-line with a low pass of 500 Hz and a high pass of 10 Hz and sampled at 2000 times per second. First the signals were integrated, rectified, and screened for movement artifacts. Second, the data were logarithmically transformed, which reduces the impact of extreme values. Third, the data were standardized (i.e., expressed as Z-scores) within subjects and muscle sites, which attenuates the undue impact of highly reactive individuals on group scores and allows meaningful comparisons across sites. EMG values for each condition were derived by taking the average activity during the 5-second period following the first second after presentation of the instructions or the stimulus (the first second was excluded to avoid artifacts resulting from muscle action associated with orienting).

Results

The first goal of the data analysis was to determine what facial muscles are activated by the external face manipulations (bite, chew) as compared to control conditions (lip and rest). The second goal was to verify what facial muscles are activated when participants produce different expressions (happy, fear, disgust, sad) when voluntarily imitating a model or responding to verbal instructions to make a particular face.

External face manipulations

The data, presented in the left panel (A) of Figure 1, were analyzed using a Manipulation (4) by Muscle (4) within-subjects MANOVA. This analysis revealed an overall main effect of the face manipulations, $F(3, 45) = 16$, $p < .001$. Post hoc paired t-tests revealed the overall activity in the bite condition was significantly greater than the lip ($p < .001$) and rest ($p < .001$) conditions. The activity in the gum condition was greater than bite ($p < .01$), rest ($p < .001$) and lip ($p < .001$). Finally, the activity in the lip condition was slightly greater than the rest condition ($p < .05$).

In addition, the above MANOVA revealed a Manipulation by Muscle interaction, $F(9, 45) = 3.48$, $p < .01$. To understand this interaction, we

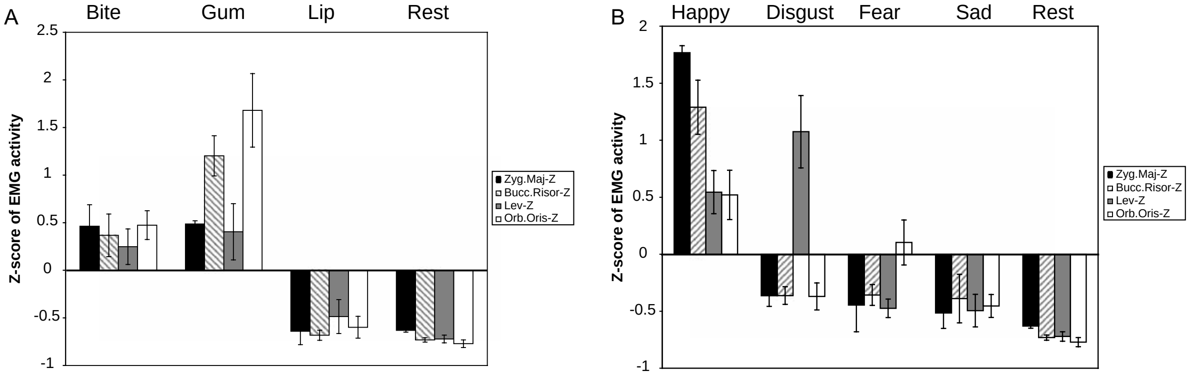

Figure 1. Standardized EMG activity during the (A) external and (B) expression experimental manipulations for Experiment 1. Bars represent the Z-score of the facial muscle activity during the (A) bite, lip, gum, and rest conditions and (B) happy, disgust, fear, sad, and rest conditions. Error bars represent the standard error of the mean.

compared relative activity of different muscles in each manipulation condition. In the bite condition, the increase in activity was distributed equally across all muscles, with all showing increased activity as compared to rest ($p < .05$) and no differences from each other. In the gum condition all muscles showed greater activity as compared to rest ($p < .05$). However, specific muscles showed greater activity than others. The orbicularis oris (lip muscle) and buccinator/risorius (cheek retractor) were enhanced when compared to zygomaticus major (cheek raiser) and levator (nose), $p < .01$. Finally, in the lip and rest conditions, there were no differences in activation across muscles.

Finally, using unfiltered data, we analyzed the temporal pattern of muscle activity caused by the gum and bite manipulations. Fast Fourier frequency spectrum analysis revealed that chewing gum generated low frequency activity, with average peak at 1.1 Hz ($SD = 0.33$). In the window between 0.5 and 1.5 Hz, the mean activity of the orbicularis oris muscle was significantly greater in the chew than bite condition ($p < .05$). The difference between the temporal patterns is illustrated in Figure 2.

In short, these data clearly suggest that facial muscles involved in producing emotional expressions are strongly activated by the bite and gum manipulations. The bite manipulation results in constantly elevated activity across muscles, whereas the gum manipulation causes most activation of muscles around the lips. Interestingly, this activity is not constant but occurs about every second. This finding is important because, as we discuss later, this pattern may allow for temporary engagement of muscles in expression-specific mimicry.

Expression manipulations

Preliminary analyses revealed no relevant effects of performing the expression to a model face compared to producing expression based on a verbal command. Therefore, subsequent analyses collapse across this manipulation.

The data, presented in the right panel (B) of Figure 1, were analyzed using Emotion (5) by Muscle (4) within-subjects MANOVA. This analysis revealed an overall main effect of condition on muscle activity, $F(4, 60) = 33.86$, $p < .001$. Post hoc paired t-tests revealed that overall level of activity in the happy condition was greater than disgust, sad, fear, and rest conditions (all $p\text{s} < .001$). Disgust condition resulted in overall more EMG activity compared to sad ($p < .01$) and rest ($p < .001$), but not fear. The fear condition was higher than rest ($p < .001$), but not sad. The sad condition was slightly higher than rest ($p < .01$).

In addition, there was an emotion by muscle interaction, $F(12, 60) = 11.42$, $p < .001$. The happy condition enhanced activation of the zygomaticus major when compared to all other muscles ($p < .001$). Additionally, buccinator/risorius was elevated when compared to the orbicularis oris ($p < .05$) and levator muscles ($p < .05$). The disgust condition selectively activated the levator, compared to other muscles ($p < .01$). The fear condition selectively activated the orbicularis oris compared to other muscles ($p < .05$). Again, the sad condition showed no significant differences in activation on any muscle, and there were no muscle differences at rest.

In short, as in earlier research, making a happy expression generated the greatest change in muscle activity, greater than any other emotion,

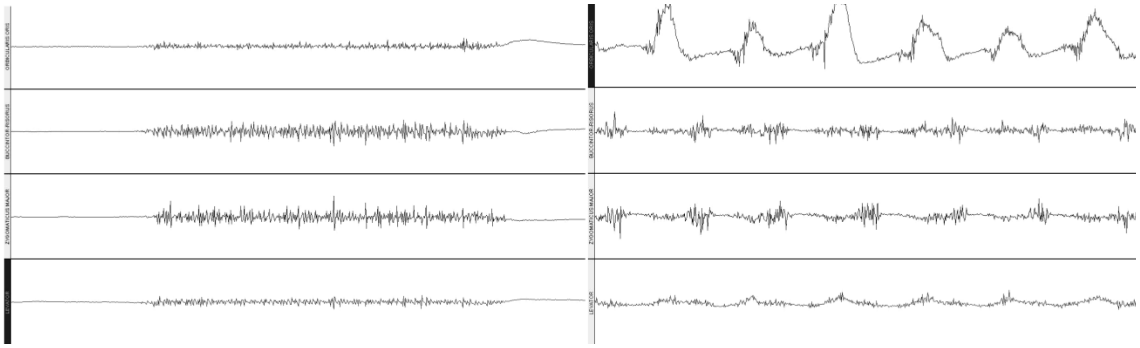

Figure 2. Examples of raw patterns of activity in the bite (left) and gum (right) condition. The muscle from top to bottom are orbicularis oris, buccinator/risorius, zygomaticus major, and levator.

with especially elevated activity of zygomaticus major and buccinator/risorius. The effects of disgust and fear expressions were limited to single muscles, levator and oris, respectively. Sadness showed no effects.

Effects of external versus expression manipulations

Finally, we compared overall levels of muscle activation generated by the external and expression manipulations. As can be seen in the left and right panels of Figure 1, the greatest level of activity was generated by the happy expression and the gum manipulation, followed by the bite manipulation. The activity generated by disgust, fear, and sadness expressions were lower than the bite, gum, and happy manipulations (all $p\text{s} <$ .001)

Discussion

Experiment 1 had two goals. The first goal was to examine effects of ''bite'' and ''gum'' manipulations that are used to prevent mimicry on muscles involved in production of facial expressions. Results showed that the bite manipulation activates all measured facial muscles, with the pattern being constant over time. The gum manipulation also activates all measured muscles, with greatest activation in the buccinator/risorius and orbicularis oris, but the pattern over time is oscillating between activity and nonactivity. The second goal of Experiment 1 was to examine muscle involvements in facial expressions. Results revealed that the happiness expression was associated with most muscle activity, especially in the classic ''cheek'' region. Disgust and fear expressions also elevated the activity but the level was weaker than happiness and was restricted to single regions (nose for disgust, lip for fear). Sadness produced no elevated activity.

EXPERIMENT 2

Experiment 2 examined the effects of the mimicry-blocking manipulation on recognition of various emotional expressions. If, as previously suggested, facial mimicry is involved in emotion recognition, then non-specific activation of muscles involved in producing a specific expression should impair recognition of that expression (Atkinson & Adolphs, 2005; Niedenthal et al., 2001).

Based on the findings from Experiment 1, one can make some more specific predictions. Recognition should be particularly impaired by the bite manipulation as it generates continuous muscle activity. Further, the bite manipulation should particularly impair recognition of happy expressions as they are associated with the greatest muscle recruitment. Given that facial muscle activity is much weaker in other facial expressions, we should see weaker effects of the bite manipulation on the recognition of disgust, fear, and especially sad.

Regarding the gum manipulation, the predictions are less clear. This manipulation strongly activates multiple facial muscles, but that activation is intermittent and therefore could allow enough activity to engage in mimicry. Further, though Pietromonaco et al. (1981) report some impairments in delayed memory for neutral expressions studies while chewing gum, there are some interpretational ambiguities with that study that suggest that effects of the gum could be due to other factors (Graziano et al., 1996).

Overview

Participants saw a series of morphed photographs taken from the Ekman–Friesen database (Ekman & Friesen, 1976). Happy, sad, fearful and disgust facial expressions were morphed to create seven levels ranging from a low level to an extreme level of each emotion. On each trial, participants were shown one face, and then given a four-alternative, forced-choice recognition task. Recognition scores were obtained during four different blocked conditions: (1) baseline, no concurrent task; (2) bite; (3) lip; and (4) gum. The instructions of the manipulation were the same as in Experiment 1. The order of the conditions was counterbalanced for each subject.

Method

Participants

A total of 12 undergraduate students (6 females, 6 males) at the University of California, San Diego, participated in this study in exchange for class credit. As this was a within-subject design, each subject participated in each of four blocks, each consisting of 280 trials. Data from 2 participants (1 male, 1 female) were not included in the analyses because their recognition scores were outliers, falling two standard deviations below the mean for multiple blocks.

Materials

Emotional photographs.. Photographs of 10 actors/models (4 male, 6 female) displaying three levels of each of four emotions, happy, sad, fear and disgust were obtained from the standard set of Ekman and Friesen (1976) and morphed to create seven levels of each emotion. This resulted in a dataset of 280 stimuli. Pilot ratings revealed that the morphed photos were recognized correctly as conveying the intended emotion at levels ranging from just slightly above chance for the low levels of the emotion to 85% correct for the extreme faces. The original set of morphs had to be edited to make lower levels of happy faces, as these were recognized at a higher level than other facial expressions—a typical finding in the emotion literature.[2] After equalizing performance across facial expressions for the pilot subjects, that set was used for the experiment. Faces were presented on the screen for a period of 500 ms followed by a screen instructing the participants to rate the facial expression as conveying happiness, sadness, fear, or disgust. The forced-choice task was self-paced and we did not collect response times. The order of presentation of the faces was randomized for each subject.

Design and procedure

The experimental design was within-subject 4 (Observed Facial Expression) × 4 (Facial Manipulation), with the order of blocks randomized. After giving written consent, participants engaged in 20 practice trials followed by four counterbalanced blocks of a four-alternative, forced-choice recognition task. During each block the participant viewed the full set of 280 stimuli while they performed no task (baseline) or engaged in one of the three facial actions (bite, chew, lip).

Results

As shown in Figure 3, despite our pretest aimed at adjusting all recognition rates to approximately the same level, the overall recognition for happy expressions was significantly lower (59%) than any of the other emotions ($p < .05$), which did not differ from each other (disgust at 71%, fear at 70%, and sad at 68%). However, note that the chance recognition for each expression was 25%, so that for each emotion there was enough room for detecting the inhibitory and facilitatory effects of external manipulations. Further, as we discuss shortly, statistically controlling for the overall recognition difficulty does not explain the impact of the mimicry manipulation.

Our primary analyses were conducted within each emotion condition and the results are shown in Figure 3. Specifically, we first conducted overall repeated measures MANOVAs with 4 levels of Manipulation Conditions (bite, gum, lip, rest), which we followed up with specific one-tailed paired-comparison tests between individual conditions. Within the happy condition there was a clear overall effect of manipulation type, $F(3, 27) = 3.52$, $p < .05$. Follow-up tests revealed that recognition of happy expressions was significantly worse during the bite condition as compared to the all other manipulation conditions combined and compared to each manipulation condition separately (all ps $< .05$). Importantly, the amount of bite-related impairment in recognition of happiness (bite minus rest) was unrelated to the participant's overall recognition performance and thus cannot be attributed to difficulty ($p > .25$).

Within disgust, there was no overall effect of manipulation type ($F < 1$). However, a paired-comparison test revealed that the bite

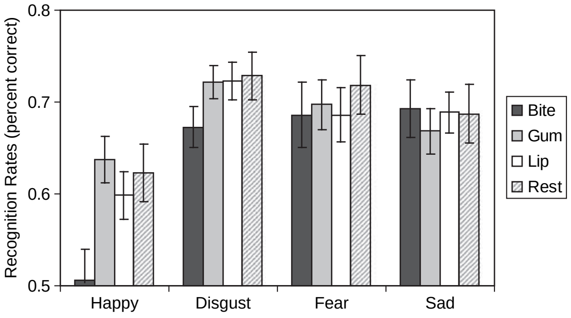

Figure 3. Recognition rates of emotional facial expressions. Bars represent the recognition rates for happy, disgust, fear, and sad facial expressions during each experimental manipulation. Error bars represent the standard error of the mean.

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[2] Very high recognition rates for happiness might account for variation in findings in some neuropsychological studies (e.g., Adolphs, Damasio, Tranel, & Damasio, 1996; Adolphs et al., 2000).

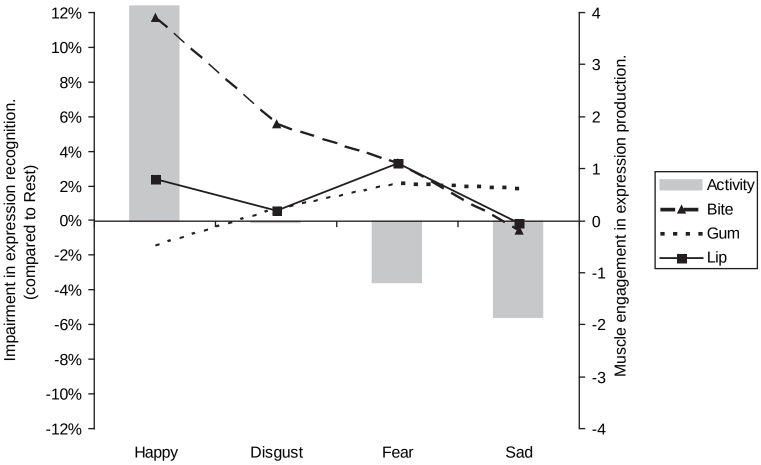

Figure 4. The relation between muscle engagement in producing an emotional facial expression and impairment in recognition of expression as a result of external face manipulation. On the right axis and shown as bars is the overall level of muscle engagement from Experiment 1. On the left axis, and shown as lines, is the relative impairment in recognition, as compared to rest, from Experiment 2.

manipulation lowered recognition of disgust when compared to the rest condition ($p < .05$), but not when compared to other conditions. There was no overall effect of manipulation type for fear ($F < 0.5$) or for sadness ($F\text{s} < 0.1$) and no specific difference between condition even approached significance.

Finally, it is interesting to relate the finding from Experiment 2 to Experiment 1 and compare the amount of impairment in expression recognition due to each manipulation (manipulation minus rest) to the overall level of muscle engagement in expression production (an average of activity across all measured muscles). Unfortunately, a proper statistical analysis is impossible as the different studies involved different subjects, thus allowing only aggregation across 4 emotion types. However, as illustrated in Figure 4, in the bite condition, the amount of recognition impairment appears positively related to the overall level of muscle engagement (i.e., most impairment for happy followed by disgust, fear, and sad). We will return to this observation in the discussion.

Discussion

Experiment 2 found that the bite manipulation specifically impairs the ability to recognize happy faces, and to some extent disgust. This finding is consistent with results from Experiment 1 that the biting manipulation (1) reliably activates several facial muscles and (2) making a happy expression generates substantial muscles activity. Experiment 2 found no reliable effects of blocking manipulations on recognition of fear and sadness, and only some indication for impairment in recognizing disgust. This finding is again consistent with Experiment 1 where these expressions generated much lower and more restricted facial activity. Reaction time (RT) data was not collected in this paradigm. Future studies including RT data would be useful to complement and clarify this finding.

One seemingly puzzling finding was the lack of interference from the gum manipulation. Apparently, college students can recognize emotions and chew gum at the same time! Jokes aside, this is puzzling as this manipulation caused strong activation of the facial muscles in Experiment 1. However, as mentioned, the chewing pattern is extremely stereotyped and occurs about every second with breaks that could allow for some muscle mimicry. The bite condition, on the other hand requires strong and continuous muscle activation, which prevents any differential muscle responses during perception.

GENERAL DISCUSSION

According to the embodiment theories, action recognition is supported by the same mental substrates as the actual performance of that same action (see Decety & Sommerville, 2003; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Evidence for this account has been provided by studies that either facilitate or interfere with motor resources and find corresponding influences on perception (e.g., Reed & Farah, 1995; Tucker & Ellis, 1998). There is also emerging evidence for the role of simulation in perception of facial expression (Goldman & Sripada, 2005).

In the current studies, we examined a unique prediction of the embodiment theories that task-irrelevant activation of motor resources should selectively interfere with perception of stimuli which draw on these resources. We tested this idea with emotional facial expressions and predicted that blocking facial muscles involved in mimicry should selectively impair recognition of emotions that engage those muscles. Consistent with these predictions, in Experiment 2 ''mimicry blocked'' participants were selectively impaired in recognition of happy faces, which activated most motor resources in Experiment 1.

Our findings extend previous research showing that disruption of facial mimicry impairs detection of transition between happy and sad facial expression (Niedenthal et al., 2001). This previous study only used two expressions morphed into a continuum and therefore could not test for emotion specificity of mimicry blocking. Our studies included two additional expressions (fear and disgust) and presented the faces one expression at a time, thus allowing for independent assessment of motor engagement in each expression. Our findings suggest that facial mimicry might be particularly important for recognizing happiness, but is less important in sadness. In addition, Niedenthal et al.'s (2001) study only had two manipulation conditions: no task and holding pen passively in the mouth. This left unclear whether possible differences between conditions (effort, distraction, etc.) could account for the results, and whether similar effects could be obtained using a manipulation that actively engaged the muscles, rather then forced participants to keep the face still (i.e., cutting out any muscular signal). Our study used a pen-biting manipulation that required an active pressure, and included an additional condition that involve a similar amount of effort (chewing gum) as well a control for possible distraction (passively holding the pen between the lips). Given the overall pattern of results, it is unlikely that our and Niedenthal et al.'s (2001) results are driven by some irrelevant factors. However, it is possible, though unlikely, that this manipulation resulted in changes in emotional states. Future studies should control for this possibility.

The recognition of happiness was most impaired by the bite manipulation. Intriguingly, happiness also showed the strongest muscle activations during imitation. This finding has interesting implications. One is that simulation of happiness engages facial musculature more than other emotions, which are simulated internally. This could be due to the fact that expression of happiness is less restricted by display rules, thus creating a particularly strong pairing between perception and action (Ekman, 2004). Importantly, the fact that recognition of disgust, fear and sadness were less affected by muscular blocking does not imply lack of simulation, but rather that their simulation may draw on different types of somatosensory resources. For example, recognition of disgust might involve simulation of interoceptive states (e.g., feeling nauseous) and recruit somatic maps in the insula (Wicker, Keysers, Plailly, Royet, Gallese, et al., 2003) whereas recognition of sadness might involve simulation of more postural components and draw more on physical body schema (Reed, 2002). The relative role of simulation of specific external and internal aspects of emotion in recognition of different expressions represents an exciting direction for future research.

It is also possible that facial mimicry depends on a system that is somatotopically specific, perhaps down to the level of utilized muscles. Although we tried to measure and manipulate the most relevant facial muscles, it is possible that we were particularly successful in interfering with muscles related to happiness. This possibility is intriguing in the light of recent research showing that the same neurons in the premotor cortex respond to both the observed and the executed action of the same somatotopic area (Buccino et al., 2001). Future studies may address this question with more focused manipulation of individual facial muscles or selective somatosensory resources.

More generally, our findings are consistent with the proposal that people's ability to understand emotions in others involves simulating their states and might be supported by the somatosensory system working in conjunction with the MNS (Atkinson & Adolphs, 2005; Gallese & Goldman, 1998). Thus, if the relevant neurons are already busy with the execution of the action, as in this study, or they are immobilized due to natural or artificial lesions, they are unable to be modulated by the observation of the same action. These suggestions are consistent with studies showing activation in the premotor cortex when participants watch people's facial expressions (Carr et al., 2003). It is also supported by research in autism. It is well known that individuals with autism spectrum disorders have difficulty understanding other people's emotional state. This impairment could be related to the fact that when viewing emotional expressions these individuals show no spontaneous activation of the mirror neuron system (Dapretto et al., 2006) and do not engage in spontaneous facial mimicry, as measured by EMG (McIntosh, Reichman-Decker, Winkielman, & Wilbarger, 2006).

In conclusion, the current results converge with previous research highlighting the contribution of embodied simulation to emotion recognition (Goldman & Sripada, 2005) and to emotion processing in general (Winkielman, Niedenthal, & Oberman, in press). More specifically, we show that impairing one's ability to use facial muscles leads to a selective deficit in the recognition of the emotions that engage those muscles. This novel finding highlights potential specificity in the simulation system underlying facial mimicry. Future studies will hopefully clarify the role of specific peripheral contributions, such as individual muscles, as well as central contribution, such as the MNS, to the observed effects.

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