Communicating emotion through facial expressions:

Social consequences and neural correlates

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Abstract

Individuals modulate their facial emotion expressions in the presence of other people. Does this *social tuning* reflect changes in emotional experiences or attempts to communicate emotions to others? Here, "target" participants underwent facial electromyography (EMG) recording while viewing emotion-inducing images, believing they were either visible or not visible to "observer" participants. In Study 1, when targets believed they were visible, they produced greater EMG activity and were more accurately "read" by observers, but did not report accompanying changes in their emotion experience. In Study 2, simultaneous facial EMG recording and fMRI scanning revealed that social tuning of targets' facial expressions correlated with activity in brain structures associated with mentalizing. These findings speak to long-standing, competing accounts of emotion expression, and suggest that individuals actively tune their facial expressions in social settings to communicate their experiences to others.

People communicate what they know, feel, and want to each other. In such communication, a "target" conveys their internal states using verbal and nonverbal cues, and an "observer" uses targets' cues to infer what targets are experiencing (1) (2) (3) (4). Effective communication between targets and observers is crucial to social life, facilitating learning (5), cooperation (6), and the formation and maintenance of relationships (7).

Facial expressions are one key channel through which targets convey their internal states to observers. Decades of research finds that targets often modulate their expressions in social settings (8) (9). For instance, facial electromyography (EMG) recordings demonstrate that targets produce larger facial movements when observers are present compared to non-social settings (10) (11). Observers judge these expressions more accurately in turn (12) (13), suggesting that they may also be more "readable." We refer to changes in facial display activity in response to the presence of others as *social tuning* of expression.

Social tuning provides a window into a long-standing debate about the meaning and function of facial emotion expressions (14). One view, which we refer to as the *experience account*, holds that facial expressions are "read-outs" of underlying emotional experience (15) (16). By this account, social tuning would occur because the presence of other people alters emotional experience—for instance intensifying positive and negative affect (17) (18)—and thus produces accompanying changes in expression. A second view, the *communication account*, posits that facial expressions represent efforts to influence others' behavior or inferences (19) (20) (21) (22). On this account, social

tuning reflects targets' attempt to change their expression in the presence of others—for instance to clearly convey their internal state (12) (13).

These theories of facial expression are not mutually exclusive, but they do make competing predictions about social tuning. The communication account—but not the experience account—predicts that when they are visible to observers, targets should alter their expressions to become more readable, even without any underlying changes in experience. Further, a communication account suggests that social tuning should be supported by cognitive processes associated with considering others' perspectives—such as "mentalizing" (23)—whereas an experience account suggests that social tuning should track other indices of emotional experience.

Social tuning thus provides an opportunity to disambiguate between experience and communication theories of facial expression. However, previous research has not clearly disentangled these accounts. In prior studies of social tuning, targets typically co-experience emotional events with observers who are also visible to them (10) (11) (12) (13) (24) (**Figure 1a**). In these contexts, social tuning could reflect communication or experience, but it could also reflect other processes. For instance, targets could mimic observers' emotions (27) (28), thus confounding multiple potential sources of social tuning.

The present research tests experience and communication accounts of facial expression through a "minimalistic" paradigm (**Figure 1b**). Targets in two studies viewed emotion-inducing images and rated their reactions under the belief that they were either visible to a close friend via video camera or not. Critically, this design manipulated the presence of observers in a manner that prevented targets from seeing

them. This ensured that social tuning did not reflect targets' responses to observers' expressions, allowing us to adjudicate between experience and communication accounts. We combined this paradigm with a multimodal assessment of targets' facial muscle activity—via facial EMG recording—and targets' emotional experience—via self-report and skin conductance responses—to test whether targets express or experience emotion differently under the belief that they are visible to an observer. We further tested whether targets who believe they are visible are more emotionally readable by examining observers' accuracy rating targets' affect across visibility conditions.

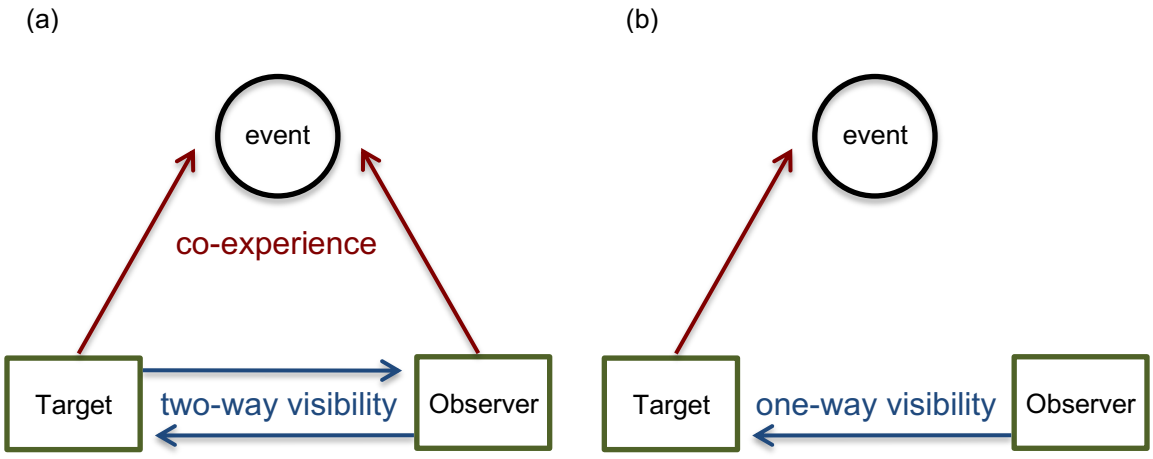

Figure 1. Social tuning task designs. (a) Previous studies have permitted two-way visibility between targets and observers as they co-experience emotional events, allowing targets to respond to how observers experience and express emotion. (b) The present "minimalistic" task manipulates targets' beliefs that they are visible to observers without permitting targets to see observers or co-experience events with them.

In Study 1, 60 pairs of friends (total $N = 120$) were randomly assigned to target or observer roles (**Figure 2a; Figure 2b**). Targets first completed a baseline phase of viewing emotion-inducing images and rating their emotional reactions under the belief that they were not visible to anyone else. Targets then completed an experimental phase in which they viewed and rated a new set of images in one of two between-subjects

conditions. Targets in the *visible* condition were informed that they would be visible to their friend—the observer—via video camera (**Figure 2c**), whereas targets in the *control* condition continued to believe they were not visible. Targets were not instructed to change their behavior in any way in either condition.

In actuality, *all targets* were video recorded throughout *both* task phases. After this task, observers viewed videos in which they could see targets' faces but not the images that targets viewed, and they inferred targets' emotions based on their facial expressions. This design enabled us to estimate interpersonal accuracy—agreement between targets' and observers' ratings of targets' experience—and to compare observers' accuracy when targets believed they were visible or not visible.

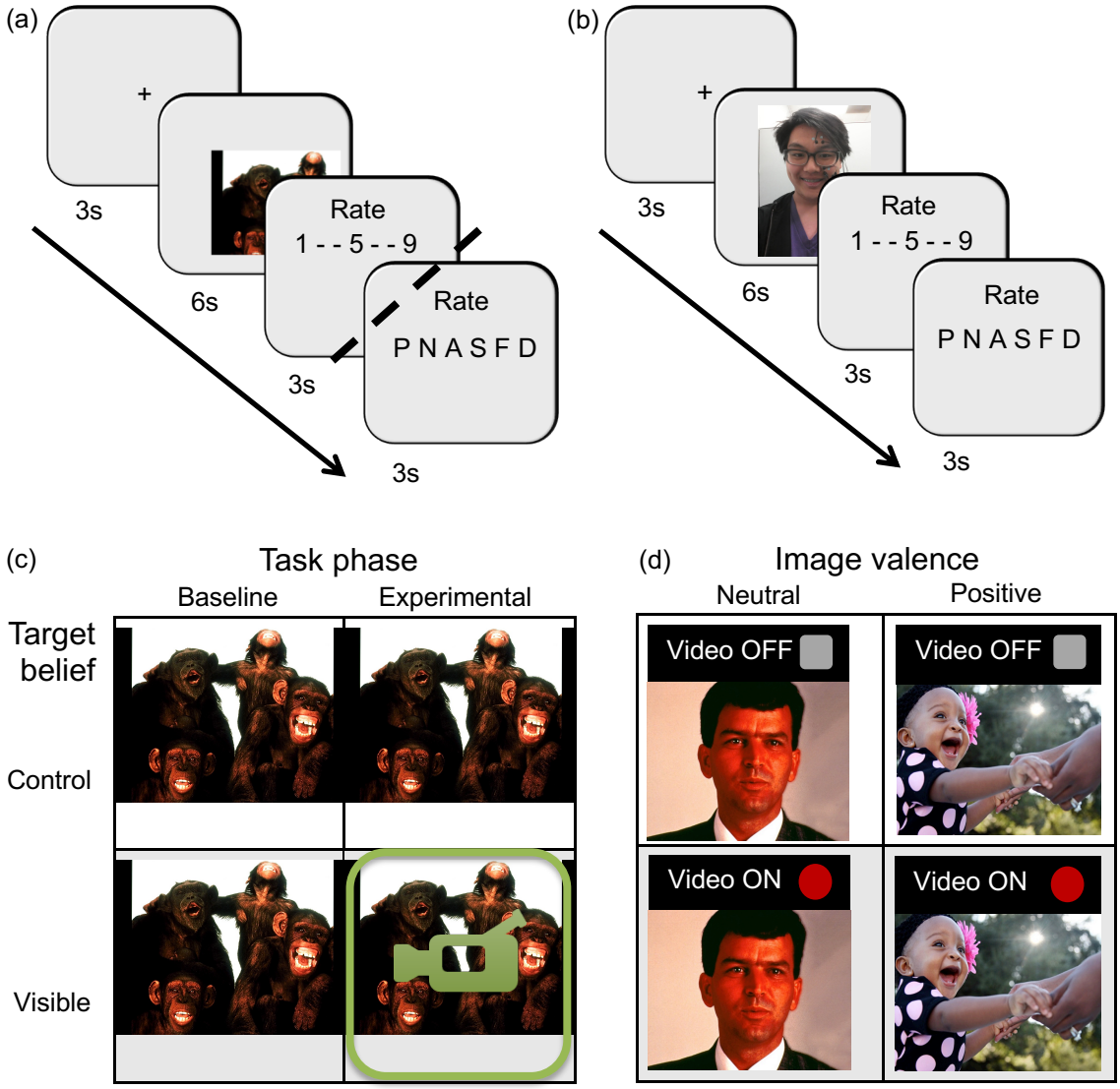

Figure 2. Social tuning task. (a) Study 1 target protocol. On each trial, targets viewed a fixation cross (3000-ms), an emotional image (6000-ms), and then rated their emotional reaction on a 9-point valence scale (3000-ms). Targets later reviewed the same images paired with an emotion category rating scale (3000-ms). (b) Study 1 observer protocol. Observers viewed a fixation cross (3000-ms), a target emotional reaction video clip (6000-ms), and then rated targets' emotional reactions on a 9-point valence scale (3000-ms), and an emotion category rating scale (3000-ms). (c) Study 1 task structure. Targets were randomly assigned to either visible or control belief conditions. At baseline, all targets viewed images under the belief that they were alone. Targets in the visible condition were informed that their friend could see them during the experimental phase only, whereas targets in the control condition completed this phase under the belief that they were still alone. (d) Study 2 task structure. Targets viewed images under the instruction that their faces were visible to a friend via video camera—on visible trials—or that the video camera was off—on control trials.

As described above, a communication account suggests that targets tune their facial expressions to communicate more clearly, likely by inferring observers' perspective and knowledge. Making such inferences—commonly referred to as "mentalizing" (23)—engages brain systems such as temporoparietal junction (TPJ), superior temporal sulcus (STS), posterior cingulate cortex (PCC), precuneus, and medial prefrontal cortex (mPFC) (27) (28). By contrast, an experience account suggests that targets may experience more intense emotions and generate larger facial expressions as "read-outs" of these changes. Individuals recruit brain systems such as the striatum, amygdala, insula, caudate, and anterior cingulate cortex, during emotional experiences (29) (30), suggesting that targets may recruit these brain systems instead.

In Study 2, we tested these hypotheses about social tuning by directly relating brain activity and facial movements. Sixteen pairs of friends took turns playing the role of target while undergoing simultaneous fMRI scanning and facial EMG recording, and were told they would later play the role of an observer trying to infer their friend's emotion. During blocks of *visible* trials, participants were told they were being video recorded and that they should clearly communicate their emotions. During blocks of *control* trials, targets were told that the video camera was off and that they should respond naturally (**Figure 2d**). We combined this design with a novel technique for directly relating brain and facial muscle activity. Specifically, we isolated brain activity that parametrically tracked facial EMG responses on an image-by-image basis, enabling us to identify neural correlates of communicating emotion through facial expressions.

Study 2 further extended Study 1 by explicitly instructing targets to communicate their emotions when they believed they were visible to observers. This manipulation

tested whether social tuning reflects targets' attempts at communicating emotion. It additionally tested whether these attempts also sharpen the clarity of targets' expressions, as predicted by a communication account. In particular, targets should produce "clearer" expressions—that more accurately represent their experience—when they communicate with observers.

Results

Study 1

Sample sizes vary across analyses due to instances in which data failed to record and where statistical outliers were excluded. We report sample sizes alongside each analysis and we detail missing cases and outlier exclusion criteria in *Data Analysis* under *Methods* for Study 1.

Facial Electromyography

We first investigated social tuning by examining whether targets in the visible, versus control, condition produced more intense facial expressions—as indicated by their facial EMG activity. Consistent with a communication account of social tuning, targets exhibited increased facial EMG activity in the visible, versus control, condition (**Table 1**).

When viewing positive images, targets in the visible condition produced greater zygomaticus EMG activity—associated with larger positive expressions (31) (32)—during the experimental phase, as compared to their own baseline, and as compared to targets in the control condition during the experimental phase ($N = 53$). Visibility

condition and task phase further interacted to predict this increased EMG activity (**Figure 3a**). Targets in the control condition showed no difference in zygomaticus EMG activity relative to baseline, and they did not differ from targets in the visible condition at baseline.

When viewing disgusting images, targets in the visible condition produced greater levator EMG activity—associated with larger disgust expressions (31) (32)—in comparison to their own baseline ($N = 56$), as shown by an interaction between visibility belief condition and task phase (**Figure 3b**). Targets in the control condition showed no difference in levator EMG activity relative to baseline, and as compared to targets in the visible condition at baseline. Overall, targets produced larger facial expressions in response to both positive and disgusting images when they knew they were visible.

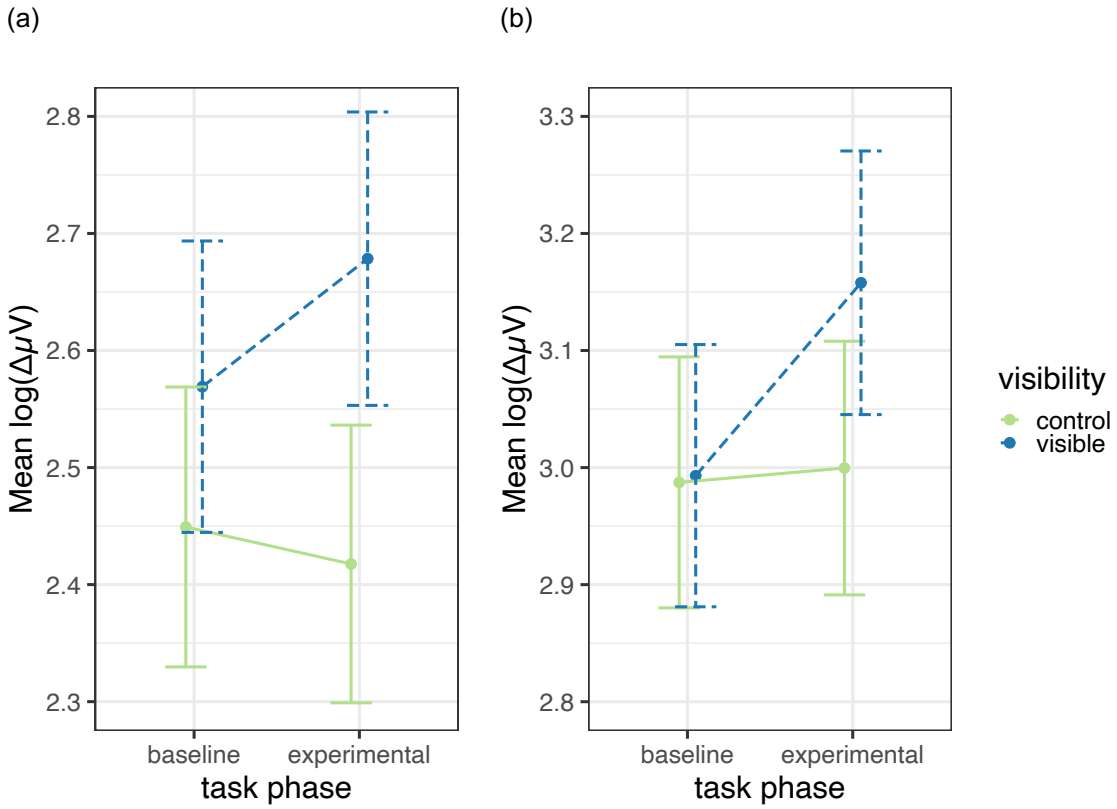

Figure 3. Mean target facial EMG activity by task phase and visibility belief condition interactions: (a) target zygomaticus EMG activity during positive image-viewing, and (b) target levator EMG activity during disgusting image-viewing. Error bars depict 95% confidence intervals.

Table 1

Visibility belief effects over target facial EMG activity.

---	*b*	*CI*	*t*
Zygomaticus (positive images)	**---**	**---**	**---**
Interaction: task phase * visibility condition	.11	[.058, .23]	3.08**
Visible targets: experimental phase > baseline	.11	[.047, .17]	3.46***
Experimental phase: visible targets > controls	.23	[.16, .30]	2.50*
Levator (disgusting images)	**---**	**---**	**---**
Interaction: task phase * visibility condition	.16	[.047, .28]	2.44*
Visible targets: experimental phase > baseline	.16	[.076, .25]	3.75***
Experimental phase: visible targets > controls	.15	[.052, .24]	1.65

Note: * $p < .05$. ** $p < .01$. *** $p < .001$. *CI* = .95.

Interpersonal Accuracy

We further tested whether observers rated targets' experiences more accurately—as indicated by the agreement between their ratings of targets' emotions and targets' own ratings—in the visible condition, versus in the control condition. In particular, we calculated the difference between observers' inferences about the emotional valence of targets' experiences, and targets' own valence ratings, on a 9-point Likert scale ranging from 'very unpleasant' to 'very pleasant' ($N = 58$). Observers rated targets in the visible condition more accurately relative to their own baseline (**Table 2**), as revealed by an interaction between visibility belief condition and task phase (**Figure 4**). Observers showed no change in their accuracy rating targets in the control condition as compared to baseline.

We next examined how accurately observers rated the valence of targets' experiences specifically when targets viewed positive images or disgusting images. When targets in the visible condition viewed positive images, observers rated their emotions more accurately (M = 2.07, SD = 1.77), in comparison to their own baseline (M = 2.43, SD = 1.93), as shown by an interaction. Observers showed no change in their accuracy rating targets in the control condition relative to their baseline, and no difference within either task phase rating targets in visible versus control conditions. When targets viewed disgusting images, observers' accuracy did not differ across task phases, by visibility belief condition, or as a function of their interaction.

To summarize, observers were more accurate about targets' emotions—and in particular their positive experiences—when targets knew they were visible.

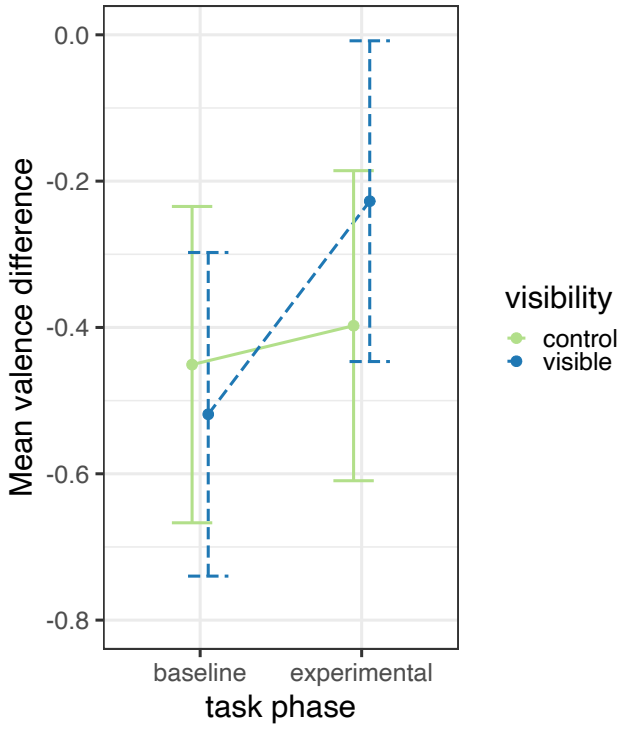

Figure 4. Mean observer interpersonal accuracy by task phase and visibility belief condition interaction: observer valence rating difference scores. Error bars depict 95% confidence intervals.

Table 2

Visibility belief effects over interpersonal accuracy: Valence difference scores.

---	*b*	*CI*	*t*
Overall	---	---	---
Interaction: task phase * visibility condition	.24	[.031, .43]	2.28*
Visible targets: experimental phase > baseline	.29	[.14, .44]	3.81***
Experimental phase: visible targets > controls	.17	[.028, .30]	1.15
Positive images	---	---	---
Interaction: task phase * visibility condition	.35	[.070, .65]	2.43*
Visible targets: experimental phase > baseline	.36	[.15, .56]	3.56***
Experimental phase: visible targets > controls	-.01	[-.20, .20]	-.03

Note: * $p < .05$. ** $p < .01$. *** $p < .001$. *CI* = .95.

Facial Electromyography Mediates Interpersonal Accuracy

Targets produced larger facial expressions when they knew they were visible and observers rated these targets' experiences more accurately. We next tested whether the effect of targets' visibility condition on observers' accuracy was mediated by targets producing larger expressions relative to baseline.

When targets viewed positive images in the visible condition ($N = 23$), observers made more accurate valence ratings relative to their baseline, $c = 0.41$, $p < .001$; these targets generated increased zygomaticus EMG activity versus their baseline, $a = 0.083$, $p = .037$; and observers made more accurate ratings of these targets as they generated increased zygomaticus EMG activity, $b = 0.72$, $p < .001$. Observers' improved accuracy rating these targets was mediated by targets' increased EMG activity, as indicated by a Sobel test showing that including targets' EMG activity in the model reduced c, $ab = .059$, $z = 1.99$, $p = .047$, 95% CI [.008, .12].

In contrast, we did not find this mediation for dyads in the control condition ($N = 28$), but moderated mediation analysis failed to detect statistically significant differences in ACME across these mediation analyses ($N = 51$), $\delta(t) = -.036$, $p = .36$, 95% CI [-.11, .044]. In a parallel set of analyses, observers were more accurate categorizing targets' experiences of positive emotion and disgust when targets knew they were visible, and this improvement was mediated by targets producing increased EMG activity at zygomaticus and levator sites respectively (**Appendix A**).

In summary, observers better understood how targets experienced positive events when targets knew they were visible, and this improved understanding was mediated by targets producing larger facial expressions.

Target Experience

Finally, an experience account of social tuning suggests that targets might experience more intense emotions in social settings, and that intensified expressions in these settings could comprise "readouts" of these experiences. To test this possibility, we examined targets' valence ratings as a measure of reported experience, and targets' skin conductance responses as a measure of physiological arousal.

Valence Ratings. Targets in the visible, versus control, condition did not report any differences in their emotional valence. There was a single interaction between visibility belief condition and task phase regarding how targets rated experiencing neutral images (N = 58) on a 9-point Likert scale ranging from 'very unpleasant' to 'very pleasant', b = .22, t = 2.87, p = .004, 95% CI [.064, .36]; but this reflected targets in the control condition experiencing neutral images as less pleasant (M = 4.97, SD = 0.87) relative to their baseline (M = 5.11, SD = 0.99), b = -.15, t = -2.92, p = .003, 95% CI [-.26, -.051].

Targets in the visible condition did not report experiencing neutral images differently from baseline and they did not differ from targets in the control condition. Targets showed no differences in how they rated experiencing positive images (N = 57) or negative images (N = 59) in response to visibility belief conditions, task phases, or their interaction.

Skin Conductance Responses. Targets further showed no differences in skin conductance responses (SCR) to viewing images with or without the knowledge that they were visible. We found a single interaction between visibility belief condition and task phase for targets producing SCRs to viewing positive images (N = 54), b = .24, t = 2.43, p =.015, 95% CI [.035, .45]; but this reflected targets in the control condition showing diminished responses to positive images (M = 4.89, SD = 0.94) versus their baseline (M = 5.15, SD = 0.93), b = -.21, t = -2.87, p = .0043, 95% CI [-.36, -.076].

Targets in the visible condition showed no difference in SCRs as compared to baseline and their responses did not differ from targets in the control condition. Targets showed no differences in producing SCRs to viewing neutral images (N = 53) or negative images (N = 53) in relation to visibility belief conditions, task phases, or their interaction.

Summary

Consistent with a communication account of facial expression of emotions, targets produced larger facial movements when they believed they were visible, but they did not show any changes in how they experienced viewing emotion-inducing images. Rather, observers rated targets' emotion more accurately when targets knew they were visible, and this improvement in their accuracy was mediated by targets producing larger expressions.

Study 2

In Study 2, we examined the neural correlates of social tuning by parametrically relating brain activity and facial EMG responses from trial to trial. This novel technique isolated

brain activity associated with producing facial expressions. In particular, we identified neural correlates of communicating emotion through facial expressions, by directing targets to convey their emotional states when cued that the video camera was on.

Participants underwent simultaneous fMRI scanning and facial EMG recording while viewing positive and neutral images under the belief that they were sometimes being video recorded. For blocks of *visible* trials, participants were told that the video camera was on—and that they should convey their emotions, whereas for blocks of *control* trials, participants were told that the video camera was off—and that they should respond naturally. This design built on Study 1 by explicitly manipulating targets' goals for emotional communication when they believed they were visible or not visible.

We further investigated whether targets produced "clearer" facial expressions when told they were visible, by examining how strongly their facial EMG responses tracked how they rated the valence of their experiences. This analysis also built on Study 1 by testing whether social tuning increases both the intensity, and the clarity, of targets' facial expressions. Three participants' data were excluded from analysis due to instrument failure and infrequent responding (final $N = 29$). We provide details on these missing cases in *Data Analysis* under *Methods* for Study 2.

Facial Electromyography

As in Study 1, targets in Study 2 generated increased EMG activity at *zygomaticus major* under the belief that they were visible to observers. Targets produced greater EMG activity in response to viewing positive images ($M = 2.05$, $SD = .30$) versus neutral images ($M = 1.97$, $SD = .27$), $b = .033$, $t = 2.45$, $p = .021$, 95% CI [.016, .056]. They also

produced greater EMG activity on visible trials than on control trials, both when viewing positive images (visible: $M = 2.12$, $SD = .31$; control: $M = 1.97$, $SD = .28$), $b = .16$, $t = 6.77$, $p < .001$, 95% CI [.14, .17]; and when viewing neutral images (visible: $M = 2.02$, $SD = .28$; control: $M = 1.92$, $SD = .26$), $b = .096$, $t = 4.67$, $p < .001$, 95% CI [.077, .12]. Being visible increased targets' EMG activity to a greater extent when they viewed positive images than when they viewed neutral images, as revealed by an interaction (**Figure 5a**), $b = .061$, $t = 4.79$, $p < .001$, 95% CI [.037, .085].

When targets believed they were visible to observers, they also produced facial EMG activity that tracked their reported experience more strongly. Targets produced EMG activity that tracked their valence ratings on visible trials, $b = .029$, $t = 10.87$, $p < .001$, 95% CI [.025, .034]; as well as on control trials, $b = .010$, $t = 3.60$, $p < .001$, 95% CI [.0047, .015]. However, targets' EMG activity tracked their valence ratings more strongly on visible trials, relative to control trials, as revealed by an interaction (**Figure 5b**), $b = .018$, $t = 6.11$, $p < .001$, 95% CI [.012, .023].

In summary, targets again produced larger facial expressions when told they were visible, but they also produced *clearer* expressions which more accurately reflected their emotion experience.

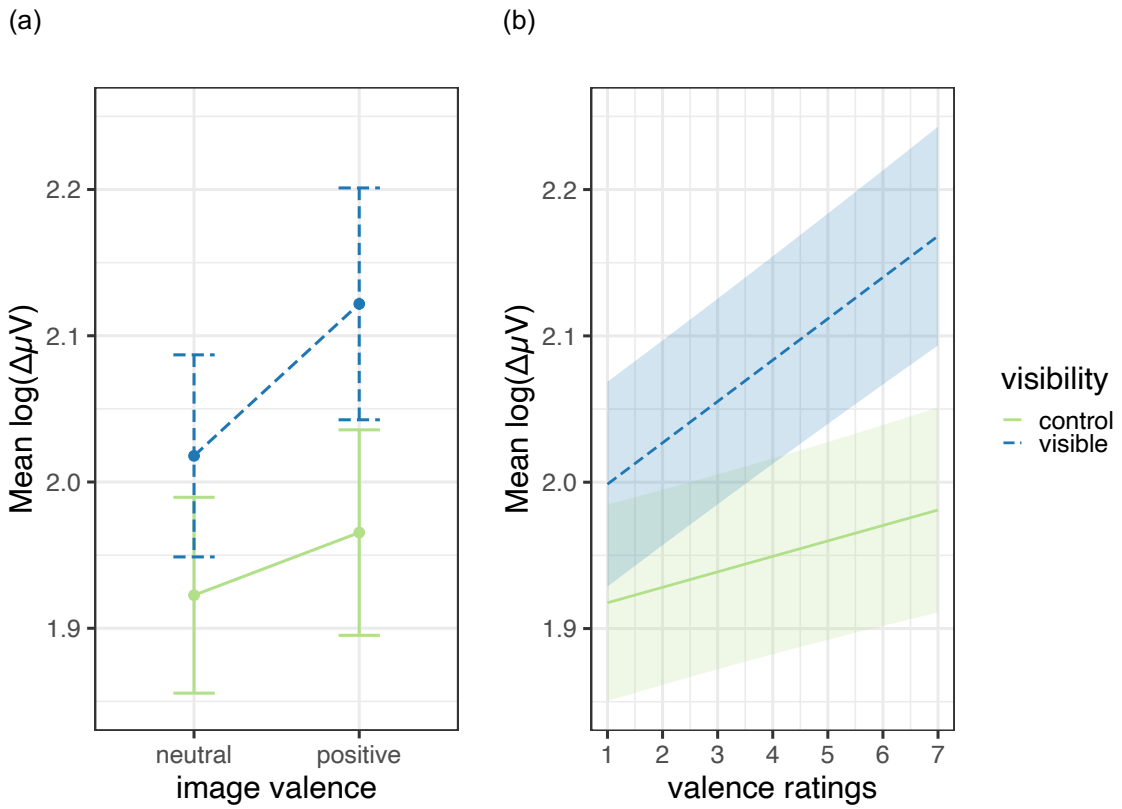

Figure 5. Mean facial EMG activity by valence and visibility belief interactions: (a) image valence and (b) valence ratings. Error bars and ribbons depict 95% confidence intervals.

Valence Ratings

Unlike Study 1, visibility beliefs also influenced how targets reported experiencing emotion in Study 2. In particular, targets reported experiencing more positive emotion in response to viewing positive images on visible trials. Targets rated their experience as more pleasant when viewing positive images ($M = 4.98$, $SD = 1.61$) than when viewing neutral images ($M = 1.62$, $SD = 1.10$) on a 7-point Likert scale ranging from 'neutral' to 'pleasant', $b = 3.34$, $t = 22.65$, $p < .001$, 95% CI [3.27, 3.42]. They also rated their experience viewing positive images as more pleasant on visible trials ($M = 5.03$, $SD = 1.64$) versus control trials ($M = 4.93$, $SD = 1.58$), $b = .10$, $t = 2.14$, $p = .032$, 95% CI

[.0036, .20]; relative to neutral images, as revealed by an interaction, $b = .19$, $t = 2.55$, $p = .011$, 95% CI [.067, .32]. Targets did not report experiencing neutral images differently across visible and control trials.

fMRI Results

Univariate Contrasts. We first examined targets' BOLD activity in response to viewing positive versus neutral images, and in response to being told they were visible. When viewing positive versus neutral images (Positive > Neutral), targets exhibited greater activity in a set of brain regions including right insula and right amygdala (**Figure 6a**; **Supplementary Table 1**). These brain structures are commonly recruited during emotional experiences (29) (30), and according to Neurosynth meta-analyses (see *Data Analysis* under *Methods* for Study 2), the coordinates of peak activity tracked emotional terms in published neuroimaging research (*z's* > 3.91; **Supplementary Table 3**).

We next examined the effects of social visibility on brain activity. According to a communication account, targets should alter their expressions in social circumstances by taking observers' perspective, whereas according to an experience account, targets generate larger expressions due to experiencing stronger emotions. When viewing images under the belief they were visible (Visible > Control), targets showed greater activity in bilateral temporoparietal junction (TPJ), bilateral posterior superior temporal sulcus (STS), posterior cingulate cortex (PCC), and precuneus (**Figure 6b**), in addition to other regions (**Supplementary Table 2**). These brain structures are commonly recruited during mentalizing (33) and their activity tracked terms related to mentalizing in Neurosynth meta-analyses (*z's* > 3.54; **Supplementary Table 3**).

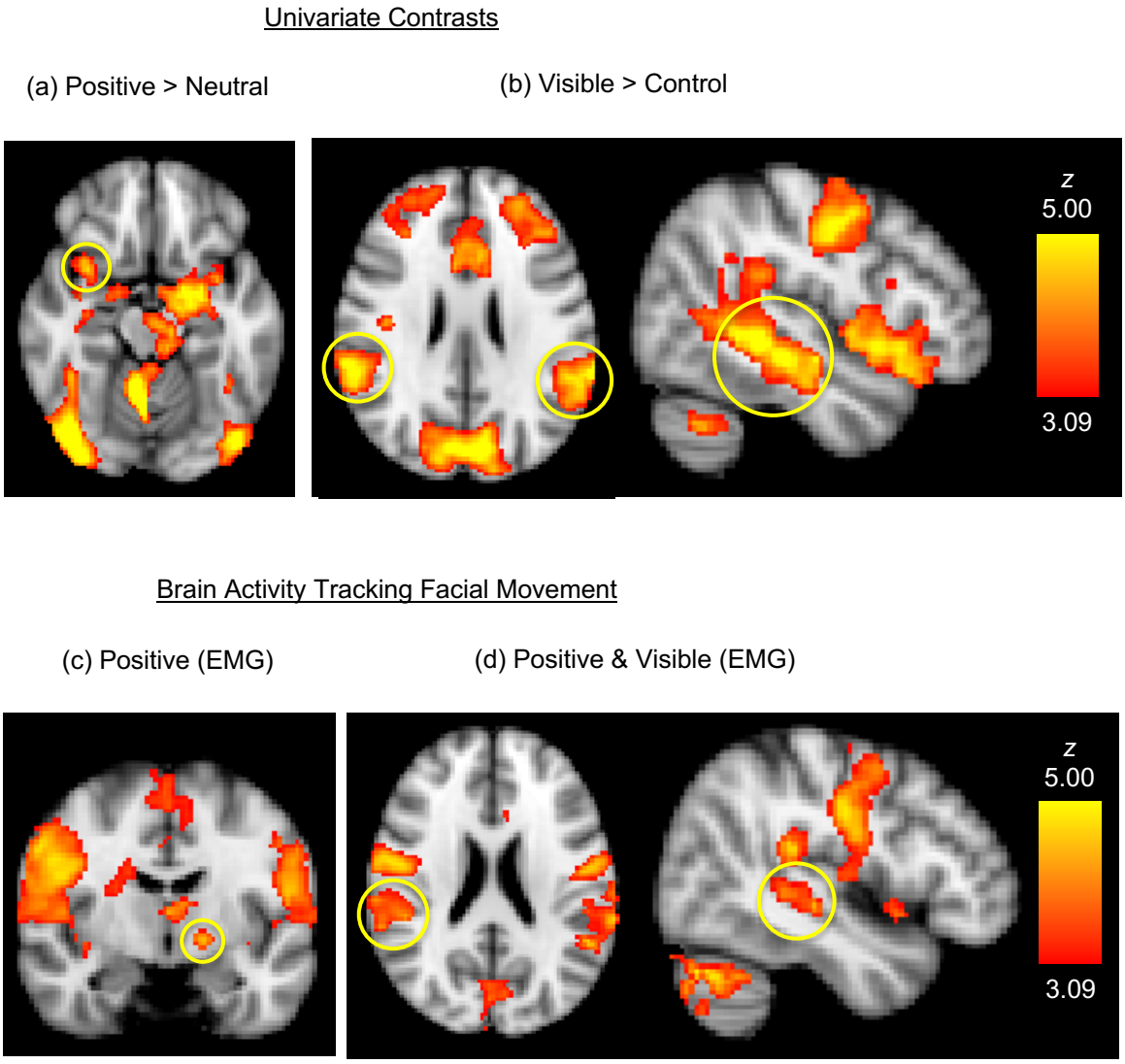

Figure 6. Differences in neural activity from univariate contrasts (top row) and parametric analyses (bottom row). Increased activity in (a) right insula during positive image-viewing (versus neutral), and in (b) bilateral temporoparietal junction (TPJ) and right superior temporal sulcus (STS) when believed to be visible (versus control). Neural activity parametrically related to EMG responsivity in (c) left ventral striatum during positive image-viewing, and in (d) right temporoparietal junction (TPJ) and right superior temporal sulcus (STS) during positive image-viewing when believed to be visible.

Brain Activity Tracking Facial Movement. We further identified brain regions whose activity parametrically varied with the facial EMG activity targets generated. Parametric contrasts coded regressors with targets' EMG responses on a trial-by-trial basis (34) and entered these regressors into general linear models that controlled for potential collinearity with image-viewing. Specifically, we demeaned EMG regressors and included regressors for univariate contrasts to effectively remove any variance shared with task manipulations (see *Data Analysis* under *Methods* for Study 2).

As a manipulation check that facial EMG activity recorded during fMRI scanning captured facial muscle movements, we conducted univariate and parametric contrasts and examined brain activity associated with producing movement. Both main effect contrasts (Positive > Neutral; Visible > Control) detected greater activity in regions of sensorimotor cortex—including supplementary motor area (SMA) and primary motor, premotor, and primary and secondary somatosensory cortices—consistent with targets generating increased facial EMG activity when they viewed positive images, and when they believed they were visible. These regions contribute to executing motor movements (35) and their activity tracked movement terms on Neurosynth (*z's* > 3.80; **Supplementary Table 3**). Likewise, in a parametric contrast collapsing across all task conditions, targets' EMG activity tracked increased activity in precuneus and sensorimotor cortex, including supplementary motor area (SMA) and right premotor and bilateral primary somatosensory cortices (**Supplementary Table 4**).

To identify brain activity associated with experiencing positive emotion, we next examined the relationship between BOLD and EMG activity for trials where targets viewed positive images. Collapsing across visible and control trials, targets' EMG

activity tracked was linked to activity in regions associated with affective experience when they viewed positive images. These regions included left ventral striatum (**Figure 6c**), right caudate, left insula, and anterior cingulate cortex (ACC; **Supplementary Table 5**). Consistent with previous meta-analyses (29) (30), these activations tracked emotional terms on Neurosynth (*z's* > 4.77; **Supplementary Table 7)**.

To further identify brain activity associated with communicating positive emotion, we examined the relationship between BOLD and EMG activity when targets viewed positive images under the belief that they were visible via video camera. Targets experienced positive affect and were instructed to convey that affect to observers on these trials. When viewing positive images on visible trials, targets produced EMG activity that tracked increased activity in right temporoparietal junction (TPJ), right anterior superior temporal sulcus (STS), and precuneus (**Figure 6d**). Following previous meta-analysis (33), these activations tracked terms related to mentalizing on Neurosynth (*z's* > 3.88; **Supplementary Table 7)**. Targets also generated EMG activity that tracked increased activity in ventral striatum among other regions (**Supplementary Table 6**). In addition, targets produced EMG activity that tracked regions of sensorimotor cortex, and these activations tracked movement terms on Neurosynth (*z's* > 3.13; **Supplementary Table 7**).

Summary

Together, these data provide support for an experience account, as targets generated larger facial expressions and reported experiencing more positive emotion when told they were visible, and this EMG activity tracked increased engagement of

ventral striatum. However, these data also support a communication account, as targets generated *clearer* facial expressions—that tracked their reported experience more strongly—under the belief that they were visible, and this EMG activity tracked greater activity within multiple regions associated with mentalizing.

Discussion

A central debate in affective science concerns the function and meaning of facial expressions. An *experience* account maintains that expressions "read-out" emotional experiences, whereas a *communication* account holds that expressions influence how other people behave. These theories are not mutually exclusive, yet they make competing predictions about social tuning, providing a powerful lens for evaluating them. The experience account suggests that social tuning reflects underlying changes in experience, whereas the communication account suggests that social tuning instead reflects targets' attempts to convey their experience to observers. Previous work had not clearly tested the distinct predictions made by each of these accounts due to confounds with free-form interactions between targets and observers.

Across two studies, we tested experience and communication accounts through a "minimalistic" task designed to clarify the meaning and function of social tuning. This task isolates targets' ability to communicate their emotions, by manipulating whether or not they believe they are visible to observers, while preventing targets from seeing observers and responding to them. In both studies, targets exhibited social tuning of emotional facial expressions. In Study 1, they produced greater facial muscle activity when they knew they were visible, and this increase in expressivity mediated observers

rating targets' experiences more accurately, without any detected change in targets' emotional experience. In Study 2, targets likewise generated more facial muscle activity when explicitly instructed to communicate their emotions. Unlike in Study 1, these targets also reported experiencing more positive emotion when visible, and their facial muscle activity also tracked increased activity in ventral striatum. However, this increased expressivity also tracked increased activity in TPJ, STS, and precuneus, in addition to tracking their reported experience more strongly.

This evidence synthesizes competing views about the nature and social functions of facial expressions. Consistent with the experience account, targets experienced more positive emotion when explicitly instructed to communicate in Study 2, and their increased expressivity tracked brain activity broadly associated with reward. However, consistent with the communication account, observers understood targets' emotions more accurately when they were visible, and targets' increased expressivity tracked brain activity broadly associated with mentalizing. In addition, targets also produced "clearer" expressions— which better reflected their emotional experience—under the explicit goal to communicate in Study 2. Overall, these findings provide evidence for experience accounts that understand facial expressions as "read-outs" of subjective experience (15) (16) and for communicative accounts that understand them as attempts to influence other people (20) (21) (22).

This work also highlights how social tuning facilitates effective communication of emotion. Observers rated targets more accurately as they produced greater facial muscle activity in Study 1, and targets generated "clearer" expressions while communicating in Study 2. Prior work had found that targets facilitate shared understanding with observers

(36) and observers rate targets' expressions more accurately when they are produced in social settings (12) (13). This work, however, had not explicitly linked how targets produce expressions and how accurately observers understand their experiences. Moreover, past research had not compared how *clearly* targets expressed themselves—how targets' expressions reflect their subjective experiences—across social and nonsocial settings. Together, these findings suggest that targets may adopt observers' perspectives, and produce facial expressions that reflect their internal states more accurately, when they wish to be understood (19) (37).

Consistent with this idea, we show in Study 2 that targets engage brain structures broadly associated with experiencing emotion and mentalizing during social tuning. By parametrically relating time-locked BOLD and facial EMG signals, we found that targets produced EMG responses tracking activity in three key sets of brain structures on a trial-to-trial basis. Across all conditions, EMG activity tracked engagement of regions within sensorimotor cortex that contribute to executing motor movements (35), providing an important manipulation check for the EMG signal. When targets viewed positive images, EMG activity tracked recruitment of left ventral striatum, right caudate, left insula, and anterior cingulate cortex (ACC), regions associated with experiencing emotion (29) (30). When targets viewed positive images under the belief that they were visible—and they were instructed to clearly convey their emotions—EMG activity tracked engagement of right temporoparietal junction (TPJ), right anterior superior temporal sulcus (STS), and precuneus, regions involved in mentalizing (33).

By providing evidence directly relating continuous measures of brain and emotion-related facial muscle activity, Study 2 produces multiple novel insights into

social tuning. In particular, we find that while producing emotional facial expressions, targets engaged brain systems similar to those associated with *perceiving* expressions—and that this activity reflected their goals for communication. Participants in previous studies have viewed emotional images and faces while undergoing combined fMRI scanning and facial EMG recording (38) (39) (40) (41). We build on this work by examining how targets generate facial expressions during live interaction with observers. In addition, previous studies have not directly related time-locked brain and facial muscle activity on a trial-by-trial basis. As a result, it has been unknown whether reported changes in brain activity actually tracked simultaneous facial movements.

By combining simultaneous fMRI and facial EMG recording with psychophysiological parametric modulation analyses, we identified brain activity that parametrically tracks facial movement on a trial-to-trial basis. This method isolates brain activity directly related to producing facial movement from brain activity that responds to task conditions but does not track facial movement. Study 2 thus addresses past limitations and provides direct evidence of brain systems that support the facial communication of emotion. Future work using this method could identify brain activity associated with producing other types of facial movements, such as those that convey negative experience, or non-facial movements such as hand gestures (42) (43).

This research further clarifies the neural mechanisms by which targets create shared understanding with observers. Targets and observers recruit similar brain systems during communication (42) (44). Specifically, their brain activity becomes temporally coupled during both verbal (45) (46), and non-verbal interaction (43) (47), including facial communication (48). When viewing and mimicking targets' expressions, observers

recruit brain systems broadly associated with mentalizing and experiencing emotion (21). By showing that targets recruit similar systems when producing expressions, this work clarifies how dyads synchronize brain activity related to experiencing emotion (48). Moreover, it suggests that dyads may also synchronize activity related to mentalizing during facial communication, as they do when communicating via eye-gaze or gesture (43) (47). Future work combining simultaneous fMRI and psychophysiological recording could investigate how dyads synchronize their brain activity, facial behavior, and peripheral physiology.

In contrast to their facial expressions, we did not find changes in how targets experienced emotion given the opportunity to communicate in Study 1. Previous work has also found targets can tune their expressions without reporting changes in their experience (10) (12), but these studies included relatively few trials and may have been underpowered to detect effects. Moreover, these studies did not record measures of targets' physiological arousal, which could change independent of their reported experience. We addressed these limitations in Study 1 but we did not find that informing targets they were visible to observers influenced their valence ratings, category ratings, or skin conductance responses. However, we found a significant effect of instructing targets to communicate in Study 2, whereby targets rated positive images as more pleasant when told they were visible. This finding is consistent with previous evidence that targets can experience more intense emotions when interacting with observers (17) (18). This effect could be explained by evidence that disclosing information about oneself is intrinsically rewarding (49), and that being understood by others enhances feelings of social connectedness (50).

This social tuning of expression may be a vital form of *interpersonal emotion regulation*—the ways in which individuals manage their own and others' emotions through social interaction (6). Individuals who openly communicate their feelings develop more supportive relationships and social networks for regulating their emotions (7). By producing expressions, targets may impact observers and the individuals with whom they interact. Indeed, emotional communications are more likely to propagate across individuals (51) and intensify in turn (52). Emotions thus transfer from person to person (53), scaffolding social interactions (37) and establishing shared reality (54). For instance, it may be intrinsically rewarding to co-experience emotions with other people (55), and individuals adjust their emotional reactions to match how other people respond (56). Future studies should directly test whether producing clear facial signals improves the social-emotional functioning of targets, observers, and their relationships.

Successful cooperation requires clear communication. Affective science has largely viewed social targets as stimuli, but in fact they are active participants in social exchange, as when they produce facial expressions to convey their internal states to observers. Consistent with this view, we find that targets produce clearer facial expressions, and that they engage brain structures that are broadly associated with mentalizing, during social interaction. From expression to perception, communication is a social endeavor.

Methods

General Method

Participants

We recruited pairs of close female friends from the Stanford University student body and local community (Study 1 total $N = 120$; Study 2 total $N = 32$). These sample sizes were pre-determined and data collection ceased once we reached these target sample sizes. All participants were at least 18 years of age (Study 1: $M = 19.89$ years, $SD = 2.93$; Study 2: $M = 20.44$ years, $SD = 2.76$). Informed consent was obtained in accordance with the Stanford University Research Compliance Office guidelines. Participants were fully debriefed about any deception and the purpose of the experiment.

Dyads of close friends were recruited given evidence that unfamiliar observers can inhibit or fail to influence facial expressions (12) (13). Both members of each dyad completed online screening inventories assessing the duration of their friendship, their weekly contact, and their relationship closeness via the Inclusion of Other in the Self Scale (IOS) (57). Dyads were required to meet the following inclusion criteria: average friendship length of at least six months (Study 1: $M = 2.07$ years, $SD = 2.79$; Study 2: $M = 1.74$ years, $SD = 1.24$), average weekly contact of at least twice per week (Study 1: $M = 5.21$ times, $SD = 1.90$; Study 2: $M = 8.90$ times, $SD = 6.85$), and average IOS score of at least 3 (Study 1: $M = 4.53$, $SD = 1.17$; Study 2: $M = 4.27$, $SD = 1.18$). See *Data Analysis* and *Results* for information on participants whose data we excluded due to technical failures and final *Ns* for each analysis.

Psychophysiological Data Acquisition and Processing

Targets' facial muscle activity was recorded via facial electromyography (EMG) at the left *zygomaticus major* (Studies 1 & 2) and *levator labii superioris* (Study 1) muscle sites. We selected these sites for their relative specificity to positive (zygomaticus) and disgust (levator) expressions (31) (32). To reduce signal impedances, facial sites were cleaned with alcohol pads, abraided with NuPrep, and washed with water. Experimenters adhered BioPac Ag/AgCl electrode pairs with electrode gel (Study 1: 4-mm; Study 2: MR-safe 11-mm) following established anatomical guidelines (58). For skin conductance responses (SCR; Study 1), targets rinsed their hands with soap and water, and experimenters adhered disposable BioPac Ag/AgCl electrode sensors with electrode gel to the middle phalanges of the third (middle) and fourth (ring) fingers of the left hand.

Psychophysiological responses were recorded and amplified with BioPac MP150 Data Acquisition Systems equipped with EMG100C Electromyogram Amplifiers and an EDA100C Electrodermal Activity Amplifier (Study 1), and an EMG100C-MRI Electromyogram Amplifier (Study 2), which reduces EPI-induced magnetic gradient switching artifact by approximately 100x (40 dB) compared to typical amplifiers. EMG activity was sampled at 1,000-Hz (Study 1 gain = 2,000; Study 2 gain = 1,000), hardware low and high pass filtered at 500-Hz and 10-Hz, and notch filtered at 60-Hz. SCR were sampled at 1,000-Hz with a gain of 5, hardware low pass filtered at 10-Hz, and notch filtered at 60-Hz. Psychophysiological recordings were processed with AcqKnowledge, the Autonomic Nervous System Laboratory (ANSLab v2.4), and custom MATLAB scripts (The Mathworks, Natick, MA). EMG data were high pass filtered at 28-Hz, low

pass filtered at 400-Hz in Study 1, comb band filtered at 60-Hz, resampled at 10-Hz, rectified, and smoothed. This high pass filter reduced electromagnetic noise generated by EPI slice acquisition at 23-Hz (46 slices per 2-second TR) in Study 2. SCR data were resampled at 25-Hz, rectified, and smoothed.

For EMG data, we calculated 1000-ms pre-stimulus proximal baseline and 2000-ms stimulus presentation averages for each trial. For SCR, we calculated 1000-ms pre-stimulus proximal baseline minima and 6000-ms stimulus presentation maxima. Proximal baseline-corrected difference scores were calculated by deducting proximal baseline values from stimulus presentation values. Difference scores were log-transformed to correct for the observed skewness inherent to EMG and SCR data. Psychophysiological data were omitted on trials where targets failed to either provide category ratings or demonstrate positive physiological difference scores.

Statistics

We tested whether instructing targets that they were visible to observers influenced (i) how much facial EMG activity targets produced, (ii) how targets experienced emotion, (iii) how accurately observers rated targets' experiences in Study 1, and (iv) how targets produced facial EMG activity that tracked their experience in Study 2. For Study 1, we tested the interactions between visibility belief condition and task phase, as only targets in the *visible* condition knew that they were visible during the experimental phase. For Study 2, we tested the interactions between visibility belief and image valence, and between visibility belief and targets' valence ratings, to compare the

effect of visibility over positive versus neutral image-viewing. Follow-up analyses tested the simple main effects of these interactions.

We conducted linear regression analyses over continuous measures (facial EMG activity, valence ratings, and SCR) and multinomial logistic regression analyses over non-continuous measures (category ratings). These mixed effect models included participant intercepts as random effects. In Study 2, image valence significantly improved model fit as a random effect slope and was included in all models, and visibility belief condition was also included as a random effect slope in all facial EMG models for significantly improving model fit. To obtain regression coefficients and 95% confidence intervals, we conducted follow-up bootstrapped regression analyses utilizing 1,000 iterations (59). Bootstrapped mediation and moderated mediation analyses likewise utilized 1,000 iterations.

Study 1

Procedure and Design

Pair members were randomly assigned to either target or observer roles but were not informed about the two roles. Instead, participants were told that they would complete two different studies and were escorted to two different testing rooms.

Target Protocol. Targets completed two 15-minute phases (72 trials each) of viewing images from the International Affective Picture System (IAPS) (60). On each trial, targets viewed an image and rated the valence of their emotional responses on a 9-point Likert scale (1 = very unpleasant; 9 = very pleasant). Targets viewed one of two image blocks over each task phase and each block included 24 different positive, neutral,

and negative images for 72 images per block. Negative images were selected to elicit disgust or fear and image blocks were balanced for valence, arousal, and social content (animacy and gender). To control for order effects, block presentation order was counterbalanced and randomized across targets, and image presentation order was randomized within each block.

Targets were randomly assigned to either visible or control belief conditions. All targets completed a baseline phase in a testing room by themselves and targets in the control condition also completed the experimental phase by themselves. Targets in the visible condition were informed—after completing the baseline phase—that they would be visible to their friend via video camera during the experimental phase. These targets were not told why they would be visible and they were not explicitly instructed to change their behavior in any way. In actuality, all targets were video recorded throughout both phases, to allow for measurements of interpersonal accuracy across task phases and visibility conditions. After the experimental phase, targets reviewed all 144 images in the same order and retrospectively assigned their *original* emotional reactions to one of six discrete emotional categories: positive, neutral, anger, sadness, fear, and disgust.

Observer Protocol. Observers completed two 18-minute phases (72 trials each) in which they watched videos of targets' reactions to each image. On each trial, observers watched a six-second video, rated the valence of targets' emotional responses on the same 9-point Likert scale (1 = very unpleasant; 9 = very pleasant), and assigned targets' emotional reactions to one of the same six discrete emotional categories. Critically, observers could see targets' reactions to each image, but not the actual images, such that they judged targets' experiences on the basis of their facial expressions.

Data Analysis

Missing Cases. Three targets' valence ratings failed to record during the baseline phase only. Instrument failure resulted in the loss of psychophysiological data in the baseline phase only for SCR (1), zygomaticus (2), and levator (1); in the experimental phase only for SCR (1), zygomaticus (2), and levator (2); and across both phases for SCR (3; $N = 57$), zygomaticus (4; $N = 56$), and levator (2; $N = 58$). In addition, we identified and removed statistical outliers from each dependent measure sample. This decision was made prior to conducting any analyses on the basis that outliers in either visible or control groups could cause failures of randomization at baseline in this between-subjects design.

Outliers. We identified outliers whose mean responses in the baseline phase differed from the sample average by more than two standard deviations (61). For targets' valence ratings, we excluded outliers when viewing positive (3; $N = 57$), neutral (2; $N = 58$), and negative images (1; $N = 59$). Likewise, we excluded outliers for targets' SCR when viewing positive (3; $N = 54$), neutral (4; $N = 53$), and negative images (4; $N = 53$). Analyses of targets' facial EMG activity excluded outliers for *zygomaticus major* when viewing positive images (3; $N = 53$) and outliers for *levator labii superioris* when viewing disgusting images (2; $N = 56$). For observers, we excluded outliers for category ratings overall (2; $N = 58$), and when viewing positive (2; $N = 58$), and disgusting images (4; $N = 56$); and outliers for valence ratings overall (2; $N = 58$), and when viewing positive (2; $N = 58$), and disgusting images (2; $N = 58$). Sample sizes vary across

analyses as follows from these omissions and all sample sizes are reported in the *Results* section alongside each analysis.

Manipulation Checks. We confirmed that targets responded to images as predicted and that observers rated targets' emotions with above chance accuracy. For continuous measures of targets' experience, we performed linear regression analyses confirming that targets rated positive images as more pleasant than neutral images, and negative images as less pleasant than neutral images, and that targets demonstrated larger SCR to positive images and negative images as compared to neutral images (**Supplementary Tables 8-10**). For targets' category ratings, we performed t-tests against chance (16.7%), confirming that targets assigned positive (68.9%), neutral (58.8%), disgusting (47.6%), and fearful (48.7%) images to their respective categories significantly above chance (**Supplementary Table 11**).

For targets' facial EMG activity, we conducted linear regression analyses confirming that targets generated greater zygomaticus activity in response to positive images (M = 2.61, SD = .67) versus neutral images (M = 2.40, SD = .51), b = -.19, t = -12.38, $p < .001$, 95% CI [-.22, -.16]; and greater levator activity in response to disgusting images (M = 3.06, SD = .52) versus neutral images (M = 2.83, SD = .43), b = .057, t = 13.97, $p < .001$, 95% CI [.049, .066]. For observers, we conducted linear regression analyses confirming that observers rated targets' reactions as more pleasant for positive images versus neutral images, and less pleasant for negative images versus neutral images (**Supplementary Tables 8-10**). Likewise, t-tests against chance (16.7%) confirmed that observers correctly categorized targets' reactions to positive (26.6%),

neutral (53.3%), and disgusting (25.5%) images, but not fearful images (8.8%), at a rate significantly above chance (**Supplementary Table 11**).

Study 2

Stimuli

In an initial pilot study, 10 pilot participants viewed 120 positive and 120 neutral images from the International Affective Picture System (IAPS) (60) and the Geneva Affective Picture Database (GAPED) (62). Item analyses determined that images of animals and people evoked larger EMG responses at the *zygomaticus major* site (M = 3.29, SD = .81) than inanimate images (M = 2.91, SD = .75), b = .38, t = 10.64, $p < .001$, 95% CI [.31, .46]. However, the IAPS image set includes relatively few positive animate images. We therefore collected positive images of infants and young animals from the internet for a second pilot study.

In a second pilot study, we presented 120 of these positive images and 120 neutral IAPS and GAPED images to 6 new pilot participants. Participants produced greater zygomaticus activity in response to the positive (M = 3.52, SD = .63) versus neutral images (M = 2.84, SD = .57), b = .68, t = 22.02, $p < .001$, 95% CI [.62, .74]. Likewise, they reported more positive experience in response to positive (M = 5.40, SD = 1.83) versus neutral images (M = 1.53, SD = 1.01) on a 7-point Likert scale, b = 3.87, t = 52.26, $p < .001$, 95% CI [3.73, 4.02].

We retained 120 of these positive images for the fMRI experiment and we used pilot participants' valence ratings to balance image blocks. Due to timing constraints,

and given our focus on the contrast of viewing positive images on visible versus control trials, we only retained 60 neutral IAPS images for the fMRI experiment.

Procedure and Design

Participants completed three 10-minute runs (60 trials each) of viewing positive and neutral images. On each trial, participants viewed either a positive or neutral image and rated the valence of their emotional response to the image on a 7-point Likert scale (1 = neutral; 7 = pleasant). Participants viewed two blocks of images over each run and each block was assigned to one of two visibility belief conditions.

For one block of each run, participants were told that their faces would be video recorded during image-viewing, as indicated by a cue displaying the words 'VIDEO ON' adjacent to a red circle at the top of the screen (63). Participants were told that their friends would later review these video recordings and rate participants' emotions. We therefore instructed participants to clearly communicate their emotions on these *visible* trials. For the other block of each run, participants were told that they would not be video recorded, as indicated by a cue displaying the words 'VIDEO OFF' adjacent to a grey rectangle at the top of the screen. We instructed participants to respond naturally while viewing images on these *control* trials. To enhance believability, we positioned an MR-safe video camera on the scanner head coil and showed participants a live video feed of their faces before the experiment. In actuality, participants were never video recorded.

Participants viewed 30 images per block (20 positive / 10 neutral) for 60 images per run (40 positive / 20 neutral). We balanced six total image blocks for image valence and we additionally balanced IAPS images for arousal and animacy. To control for block

order effects, block presentation order was randomized across participants. Within each block, image presentation order and jitter duration were pseudo-randomized to optimize statistical power for fMRI analyses. We generated six different optimized image valence/jitter sequences using optseq2 and randomized these sequences across the six image blocks for each participant (64). This preset the order in which participants viewed positive and neutral images but randomized *which* image appeared on each trial. Image presentations were time-locked to 2000-ms TRs.

We further randomized the six image blocks and six image valence/jitter sequences across the visible and control conditions such that participants viewed three blocks of images under each condition. To control for visibility belief condition order effects, we counterbalanced condition order across participants. Here, we generated six possible visibility belief condition orders that ensured (i) each run included one block of visible trials and one block of control trials, (ii) participants never viewed more than two consecutive image blocks under the same visibility belief condition, and (iii) participants never completed more than two runs of image-viewing in the same visibility belief condition order. Following the main experiment, participants underwent an anatomical MRI scan.

Neuroimaging Acquisition and Processing

We recorded functional imaging data on a 3-T General Electric MR750 scanner with a gradient-echo echo-planar-imaging sequence (46 axial slices of 2.9-mm^3 voxels; TR = 2000-ms; TE = 25-ms; 80x80 matrix; flip angle 90°; FOV 23.2x23.2-cm), followed by a high-resolution T1-weighted anatomical scan (186 axial slices of 0.9-mm^3 voxels;

TR = 7.2-ms; TE = 2.8-ms; 256x256 matrix; flip angle 12°; FOV 25.6x23.2-cm). MRI data were preprocessed and analyzed in FSL (65). To ensure stabilization, the first 4 TRs were discarded. Functional data were motion corrected with MCFLIRT, slice-time corrected for interleaved acquisition, brain extracted with BET, spatially smoothed (5-mm), high-pass temporally filtered (100-s cutoff), registered to anatomical scans (6 DOF), and transformed to standard structural space (12 DOF) with Brain Template 152 from the Montreal Neurological Institute (MNI).

Data Analysis

Missing Cases. One participant's fMRI data failed to record due to instrument failure and two participants failed to respond to more than 20% of total trials. We excluded these three participants' data from all analyses (final $N = 29$).

BOLD Data. Functional scans were analyzed through mixed effect general linear models (GLMs). We convolved regressors with a canonical gamma hemodynamic response function (lag M = 6-s, SD = 3) and applied temporal filtering. All GLMs used FILM prewhitening and included confound regressors for temporal derivatives, standard motion parameters, and motion outliers. We ran second-level analyses over each participant's three first-level analyses, group-level analyses (FLAME 1) over second-level analyses, and applied a cluster-defining threshold of $z > 3.09$ ($p < .001$) with FWE correction ($p < .05$) as a stringent parametric correction for multiple comparisons (66).

Univariate contrasts examined the main effects of image valence (Positive > Neutral) and visibility belief (Visible > Control) manipulations. To ensure that image valence and visibility belief contrasts reflected main effects only, GLMs examining

univariate contrasts included a regressor coding their interaction, effectively removing any variance shared between main effects and the interaction. Parametric contrasts identified brain activity tracking facial EMG responses (34) (67) (68). GLMs examining parametric contrasts controlled for potential collinearity with BOLD responses to image-viewing in two ways.

First, to eliminate collinearity with the image-viewing task, EMG regressors were demeaned for each run (69). Second, to control for collinearity with task manipulations, relevant task contrast regressors were included whenever EMG regressors spanned multiple task conditions. Specifically, we included main effect and interaction regressors when examining EMG overall and simple main effect regressors when examining EMG during positive image-viewing. These controls ensured that EMG regressors reflected parametric relationships only, by effectively removing any variance shared with main effect or interaction regressors. For each BOLD contrast, we report the coordinates of activation peaks and relevant terms associated with coordinates in Neurosynth meta-analyses of published neuroimaging research (70).

Author Contributions

W.C.W. contributed to study design, data acquisition, data analysis, and manuscript preparation. Y.C.L. and E.A.C. contributed to data analysis. E.C.N. contributed to study design and implementation. J.S. contributed to data acquisition. J.Z. contributed to study design and manuscript preparation. All authors provided comments and approved of the final manuscript.

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Supplementary Table 1

Main effect of image valence: Positive > Neutral.

Region	*Z* score	*x*	*y*	*z*
Left primary motor cortex	7.57	-30	-24	66
Left primary somatosensory cortex	7.46	-52	-24	50
Right cerebellum	7.45	16	-52	-24
Right middle temporal visual area (v5)	7.31	50	-74	0
Left occipital cortex	6.57	-48	-80	-4
Right cerebellar vermis	6.38	12	-64	-50
Precuneus	5.88	4	-62	40
Left middle temporal visual area (v5)	5.86	-50	-80	2
Left fusiform face area	5.70	-44	-78	-16
Right primary motor cortex	5.53	44	-8	32
Left cerebellum	4.87	-46	-54	-32
PCC	4.85	4	-54	24
Right medial temporal cortex	4.77	32	-6	-42
Right insula	4.72	34	10	-16
Right caudate	4.67	20	-22	22
Left inferior occipital cortex	4.65	-36	-84	-22
Right temporal pole	4.58	26	12	-28
Right anterior temporal cortex	4.56	36	0	-42
Right anterior hippocampus	4.39	30	20	-34
Right amygdala	4.28	32	-4	-24
Left dorsolateral prefrontal cortex	3.59	-32	42	16

Note: Cluster-defining threshold $z > 3.09$ ($p < .001$) with FWE correction $p < .05$. Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.

Supplementary Table 2

Main effect of visibility belief condition: Visible > Control.

Region	*Z* score	*x*	*y*	*z*
SMA	6.96	-2	4	58
Right occipital cortex	6.13	16	-88	32
Left posterior insula	6.05	-44	6	-6
Right posterior STS	5.89	46	-36	-2
Right anterior STS	5.82	50	-26	-10
Left secondary somatosensory cortex	5.79	-50	0	2
Left occipital cortex	5.78	-2	-82	26
Right TPJ	5.7	64	-38	34
Right posterior parietal cortex	5.68	60	-38	30
Right ventral striatum	5.68	20	10	-6
Left anterior insula	5.63	-42	18	-10
Right cerebellum	5.62	32	-58	-36
Left primary motor cortex	5.57	-50	-12	40
Right secondary somatosensory cortex	5.55	56	10	0
Left cerebellum	5.53	-36	-56	-36
PCC	5.51	-4	-16	38
Right premotor cortex	5.37	52	-4	44
Left posterior parietal cortex	5.35	-64	-42	24
Left premotor cortex	5.33	-54	-8	42
Left TPJ	5.05	-54	-52	20
Precuneus	5.05	-2	-50	54
ACC	5.02	6	16	28
Left anterior STS	4.52	-44	-54	4
Brainstem	4.46	6	-36	-40
Left inferior parietal lobule	4.44	-56	-48	42
Right dorsolateral prefrontal cortex	4.4	32	32	24
Left posterior STS	4.12	-60	-62	6

Note: Cluster-defining threshold $z > 3.09$ ($p < .001$) with FWE correction $p < .05$. Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.

Supplementary Table 3

Neurosynth terms associated with brain activity: Univariate contrasts.

Region	Term	*Z* score
Image valence (Positive > Neutral)	**---**	**---**
Left primary motor cortex	movement	10.51
Left primary somatosensory cortex	motor task	7.43
Right cerebellum	movements	12.02
Right cerebellar vermis	movements	5.85
Right primary motor cortex	production	9.03
Left cerebellum	motor performance	4.39
Right insula	emotional information	3.91
Right amygdala	emotional	12.54
Visibility belief (Visible > Control)	**---**	**---**
SMA	movements	7.37
Right posterior STS	social	4.70
Right anterior STS	theory mind	4.69
Left secondary somatosensory cortex	movements	4.60
Right TPJ	resonance compare	4.40
Right cerebellum	motor	4.33
Left primary motor cortex	movement	5.95
Right secondary somatosensory cortex	movement	4.96
Left cerebellum	movements	3.80
PCC	social	3.54
Right premotor cortex	movements	9.84
Left premotor cortex	movements	6.87
Left TPJ	theory mind	9.08
Precuneus	mentalizing	3.58
Left posterior STS	actions	4.05

Supplementary Table 4

EMG parametric contrast collapsing across all task conditions.

Region	*Z* score	*x*	*y*	*z*
Left primary somatosensory cortex	5.41	-46	-16	32
Left primary auditory cortex	5.14	-58	-32	16
Right premotor cortex	5.13	56	-2	36
Precuneus	4.94	-2	-82	40
SMA	4.52	10	8	66
Right primary somatosensory cortex	4.47	64	-28	28
Right primary auditory cortex	4.46	58	-2	4
Right cerebellum	4.38	6	-74	-20
Left cerebellum	4.36	-20	-62	-26
Cuneus	3.85	-8	-76	24

Note: Cluster-defining threshold $z > 3.09$ ($p < .001$) with FWE correction $p < .05$. Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.

Supplementary Table 5

EMG parametric contrast during positive image-viewing.

Region	*Z* score	*x*	*y*	*z*
Right premotor cortex	5.85	56	-4	38
Right cerebellum	5.40	50	-60	-34
Cuneus	5.16	10	-82	40
Left primary somatosensory cortex	5.07	-46	-16	32
Left primary auditory cortex	4.88	-58	-32	16
Precuneus	4.81	0	-80	40
SMA	4.77	8	4	70
Right primary motor cortex	4.76	50	-12	34
Right secondary somatosensory cortex	4.63	64	0	14
Right posterior parietal cortex	4.62	60	-38	26
Left cerebellum	4.59	-40	-78	-34
Thalamus	4.58	0	-22	10
Left ventral striatum	4.46	-16	-8	-4
Right TPJ	4.41	62	-40	22
Left insula	4.41	-36	2	4
Left thalamus	4.41	-16	-20	0
Right primary somatosensory cortex	4.29	46	-32	16
Left primary motor cortex	4.27	-56	-8	32
Left secondary somatosensory cortex	4.26	-66	-32	30
ACC	3.83	-6	20	24
Right caudate	3.70	18	-4	24
Right superior parietal cortex	3.55	26	-40	68

Note: Cluster-defining threshold $z > 3.09$ ($p < .001$) with FWE correction $p < .05$. Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.

Supplementary Table 6

EMG parametric contrast during positive image-viewing when believed visible.

Region	*Z* score	*x*	*y*	*z*
Right premotor cortex	5.99	56	-4	36
Right cerebellum	5.52	4	-76	-20
Cuneus	4.99	12	-82	40
Left cerebellum	4.85	-38	-78	-34
Left primary somatosensory cortex	4.83	-46	-16	32
SMA	4.79	10	4	62
Left secondary somatosensory cortex	4.72	-54	-8	18
Left primary auditory cortex	4.69	-66	-36	22
Right primary somatosensory cortex	4.68	46	-32	18
Thalamus	4.63	0	-8	8
Right secondary somatosensory cortex	4.47	62	2	6
Right anterior STS	4.39	46	-24	-4
Right TPJ	4.19	62	-40	22
Left ventral striatum	4.10	-16	-8	-4
Right superior parietal cortex	3.86	20	-50	70
PCC	3.85	0	-46	12
Precuneus	3.26	8	-40	54

Note: Cluster-defining threshold $z > 3.09$ ($p < .001$) with FWE correction $p < .05$. Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.

Supplementary Table 7

Neurosynth terms associated with brain activity: EMG parametric contrasts.

Region	Term	*Z* score
All task conditions	**---**	**---**
Left primary somatosensory cortex	production	5.19
Right premotor cortex	movements	6.31
Precuneus	mind tom	3.74
SMA	movement	3.56
Right primary somatosensory cortex	movement	4.50
Right cerebellum	movements	5.44
Left cerebellum	movement	6.91
Positive image-viewing	**---**	**---**
Right premotor cortex	movements	6.53
Right cerebellum	tapping	4.30
Left primary somatosensory cortex	production	5.19
SMA	movements	4.90
Right primary motor cortex	production	9.41
Right secondary somatosensory cortex	production	5.03
Left ventral striatum	monetary reward	4.77
Left insula	affective	5.34
Right primary somatosensory cortex	motor	3.40
Left primary motor cortex	movement	3.83
Left secondary somatosensory cortex	motor	3.13
ACC	fear	5.47
Right caudate	monetary reward	4.80
Positive image-viewing when believed visible	**---**	**---**
Right premotor cortex	movements	5.41
Right cerebellum	movements	5.20
Left cerebellum	motor performance	5.06
Left primary somatosensory cortex	motor	4.65
Left secondary somatosensory cortex	motor	3.36
Right primary somatosensory cortex	motor	4.51
Right secondary somatosensory cortex	motor	4.07
Right anterior STS	speech	8.21
Right TPJ	action observation	7.44
Left ventral striatum	monetary reward	4.77
Precuneus	person	3.88

Supplementary Table 8

Descriptive statistics: Valence ratings and skin conductance responses by image valence.

---	**Positive**		**Neutral**		**Negative**	
---	*M*	*SD*	*M*	*SD*	*M*	*SD*
Targets	**---**	**---**	**---**	**---**	**---**	**---**
Valence ratings	7.23	1.23	5.06	.97	2.66	1.43
Skin conductance responses	4.85	1.04	4.81	1.01	4.87	1.03
Observers	**---**	**---**	**---**	**---**	**---**	**---**
Valence ratings	5.01	1.78	4.36	1.43	3.96	1.64

Note: Skin conductance responses are log-transformed.

Supplementary Table 9

Manipulation checks: Positive vs. neutral linear regression analyses.

---	*b*	*CI*	*t*
Targets	**---**	**---**	**---**
Valence ratings	-2.11	[-2.17, -2.05]	-68.90***
Skin conductance responses	-.079	[-.15, -.0087]	-2.22*
Observers	**---**	**---**	**---**
Valence ratings	-.66	[-.74, -.58]	-14.93***

Note: * $p < .05$. ** $p < .01$. *** $p < .001$. *CI* = .95.

Supplementary Table 10

Manipulation checks: Negative vs. neutral linear regression analyses.

---	*b*	*CI*	*t*
Targets	**---**	**---**	**---**
Valence ratings	-2.39	[-2.45, -2.32]	-70.57***
Skin conductance responses	.097	[.024, .16]	2.75**
Observers	**---**	**---**	**---**
Valence ratings	-.37	[-.44, -.29]	-9.26***

Note: * $p < .05$. ** $p < .01$. *** $p < .001$. *CI* = .95.

Supplementary Table 11

Manipulation checks: Category ratings vs. chance t-test analyses.

---	*d*	*CI*	*t*
Targets	**---**	**---**	**---**
Positive	.52	[.50, .54]	46.86***
Neutral	.42	[.40, .45]	36.49***
Disgust	.092	[.061, .12]	6.04***
Fear	-.084	[-.11, -.062]	-6.91***
Observers	**---**	**---**	**---**
Positive	.10	[.076, .12]	8.90***
Neutral	.37	[.34, .39]	29.54***
Disgust	.088	[.050, .12]	4.68***
Fear	-.077	[-.11, -.049]	-5.43***

Note: * $p < .05$. ** $p < .01$. *** $p < .001$. *CI* = .95.

Appendix A

Study 1 Emotion Category Analyses

Targets and observers also assigned targets' experiences to one of six discrete emotional categories: positive, neutral, anger, sadness, fear, and disgust. Whereas valence ratings indexed the emotional intensity of targets' experiences, category ratings indexed the emotional quality of their experiences. In a parallel set of analyses, we estimated the agreement between targets' and observers' category ratings—as a second measure of interpersonal accuracy, we related this agreement to targets' EMG activity through mediation analyses, and we analyzed targets' category ratings—as an additional measure of their experience.

Interpersonal Accuracy

To assess how well observers understood the emotional quality of targets' experiences, we examined the extent to which their emotion category ratings agreed with targets' own emotion category ratings ($N = 58$). Observers rated targets in the visible condition more accurately—as indicated by more frequent agreement with targets' category ratings—in comparison to baseline (**Table A1**), as revealed by an interaction between visibility belief condition and task phase (**Figure A1a**).

Having found that targets amplified their positive and disgust expressions when they knew they were visible, we further examined how accurately observers categorized targets' emotions when targets viewed positive images ($N = 58$) or disgusting images ($N = 56$). When targets in the visible condition viewed positive images, observers rated their emotions more accurately—as indicated by correctly categorizing their positive

experiences more often—versus baseline and versus targets in the control condition, as shown by an interaction. Observers showed no change in their accuracy rating targets in the control condition relative to baseline, and no difference rating targets in visible versus control conditions at baseline. Although the interaction was not significant, when targets in the visible condition viewed disgusting images, observers again rated their emotions more accurately—as indicated by correctly categorizing their disgust experiences more frequently—versus baseline and versus targets in the control condition. Observers did not show changes from baseline in their accuracy rating targets in the control condition.

In sum, observers better understood the quality of targets' emotions—and specifically how they experienced positive emotion and disgust—when targets knew they were visible.

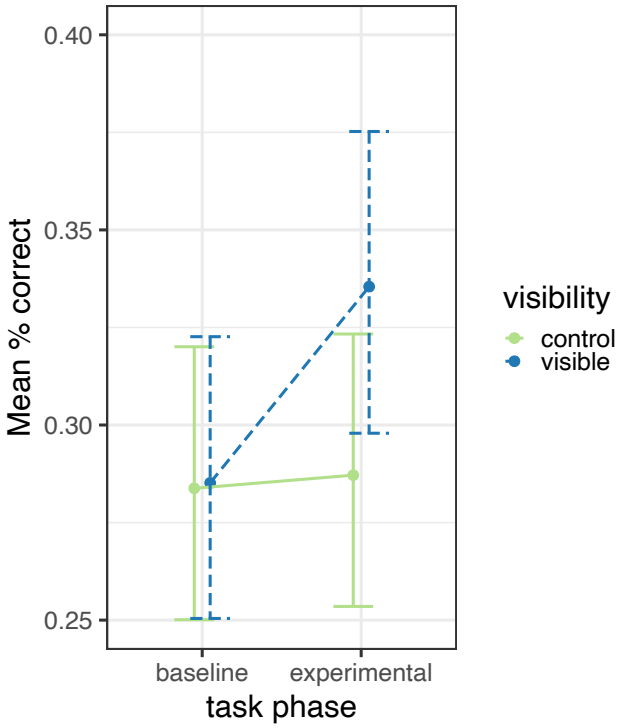

Figure A1. Mean observer interpersonal accuracy by task phase and visibility belief condition interaction: observer category rating accuracy scores. Error bars depict 95% confidence intervals.

Table A1

Visibility belief effects over interpersonal accuracy: Category accuracy scores.

---	*b*	*CI*	*z*
Overall	**---**	**---**	**---**
Interaction: task phase * visibility condition	.22	[.016, .42]	2.22*
Visible targets: experimental phase > baseline	.24	[.10, .37]	3.32***
Experimental phase: visible targets > controls	.24	[.10, .39]	1.77
Positive images	**---**	**---**	**---**
Interaction: task phase * visibility condition	.51	[.11, .90]	2.55*
Visible targets: experimental phase > baseline	.31	[.058, .55]	2.35*
Experimental phase: visible targets > controls	.92	[.63, 1.20]	3.78***
Disgusting images	**---**	**---**	**---**
Interaction: task phase * visibility condition	.45	[-.20, 1.17]	1.38
Visible targets: experimental phase > baseline	.53	[.077, .96]	2.28*
Experimental phase: visible targets > controls	.79	[.30, 1.29]	2.36*

Note: * $p < .05$. ** $p < .01$. *** $p < .001$. *CI* = .95.

Facial Electromyography Mediates Interpersonal Accuracy

Zygomaticus Major

When viewing positive images, targets produced increased zygomaticus EMG activity when they knew they were visible, and this mediated observers rating their positive experiences more accurately. For category ratings, observers rated targets in the visible condition ($N = 25$) more accurately as compared to baseline, these targets produced increased zygomaticus EMG activity relative to baseline, and observers rated these targets more accurately as they produced increased zygomaticus EMG activity (**Figure A2a**). Observers rating these targets more accurately was mediated by targets

producing increased EMG activity, as revealed by a Sobel test showing that including targets' EMG activity in the model reduced *c, ab* = .043, $z = 3.25$, $p < .001$, 95% CI [.019, .069]. This mediation was moderated by visibility belief condition such that we found this mediation for dyads in the visible condition, but not for dyads in the control condition ($N = 27$), as indicated by a moderated mediation analysis ($N = 52$) showing differences in the average causal mediation effects (ACME) across these mediation analyses, $\delta(t) = -.035$, $p = .004$, 95% CI [-.061, -.010].

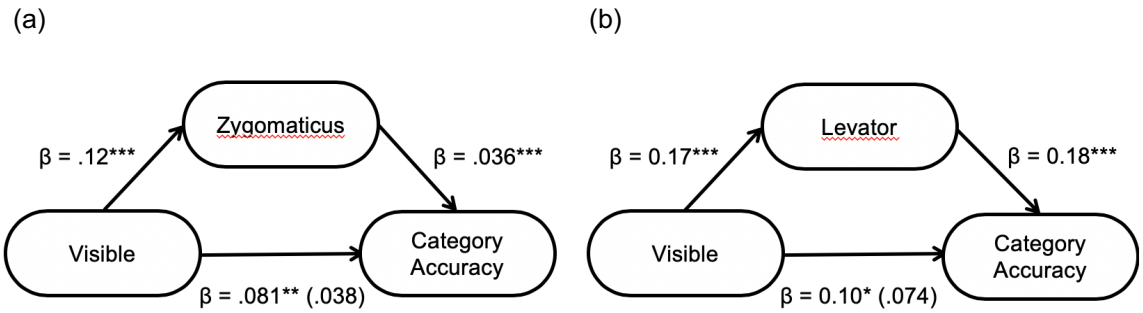

Figure A2. Target facial EMG activity mediates the effect of target visibility beliefs over observer category rating accuracy: mediation by (a) zygomaticus EMG activity during positive image-viewing, and (b) levator EMG activity during disgusting image-viewing. Note: * $p < .05$. ** $p < .01$. *** $p < .001$.

Levator Labii Superioris

When viewing disgusting images, targets generated increased levator EMG activity when they were informed that they were visible, and this mediated observers categorizing their disgust experiences more accurately. Observers made more accurate category ratings of targets in the visible condition ($N = 25$) in comparison to baseline, these targets generated increased levator EMG activity relative to baseline, and observers made more accurate category ratings as targets generated increased levator EMG activity (**Figure A2b**). Observers making more accurate category ratings was mediated by

targets generating increased EMG activity, as demonstrated by a Sobel test finding that including targets' EMG activity in the model reduced *c*, $ab = .031$, $z = 2.51$, $p = .012$, 95% CI [.0090, .059]. This mediation was moderated by visibility belief condition in that we detected mediation for dyads in the visible condition, but not for dyads in the control condition ($N = 28$), as shown by a moderated mediation analysis ($N = 53$) finding variation in ACME across these mediation analyses, $\delta(t) = -.026$, $p = .014$, 95% CI [-.049, -.0044].

Target Experience

Targets did not show any differences in how they assigned their experiences to one of six emotion categories depending upon whether or not they knew they were visible ($N = 60$). We detected a single interaction between visibility belief condition and task phase concerning how targets categorized experiencing neutral images as neutral vs. positive, $b = -.37$, $z = -1.97$, $p = .049$, 95% CI [-.75, -.0062]; however, targets showed no differences in how they categorized experiencing neutral images as neutral vs. positive between visible and control conditions or relative to baseline. Targets further showed no differences in how they categorized experiencing positive images as positive vs. neutral, or how they categorized experiencing negative images as negative vs. neutral, as a function of visibility belief conditions, task phases, or their interaction.