Running head: NEURAL CORRELATES OF FACIAL EXPRESSIONS

Neural correlates of communicating emotion through facial expressions:

A simultaneous fMRI and facial EMG study

W. Craig Williams*, Yuan Chang Leong, Eleanor A. Collier & Jamil Zaki

Department of Psychology, Stanford University

*Address correspondence to:

W. Craig Williams
Department of Psychology, Stanford University, Stanford, CA 94305
wcwill@alumni.stanford.edu

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Abstract

People commonly communicate emotional states through facial expressions. However, existing neuroimaging research focuses almost entirely on brain systems involved in *perceiving* expressions, leaving unclear whether similar systems are recruited when people *generate* expressions. Pairs of friends took turns viewing positive and neutral images while undergoing simultaneous fMRI scanning and EMG recording of *zygomaticus major*, a facial muscle associated with smiling. Participants were instructed that they were either visible to their friend or not visible during image-viewing. When participants viewed positive images, their EMG responses parametrically tracked activity in brain structures associated with experiencing emotion, including ventral striatum, caudate, insula, and anterior cingulate cortex. When further instructed that they were visible to their friend, participants' EMG responses also tracked activity in structures associated with mentalizing, including temporoparietal junction, superior temporal sulcus, and precuneus. These findings suggest that neural systems involved in perceiving facial expressions also support their production during communication.

People ubiquitously convey what they know, feel, and want to each other. Such communication is typically modeled as involving a “target” and an “observer” (Pickering & Garrod, 2004). Targets convey their internal states using cues such as facial expressions, body positioning, language, and prosody (Barrett, Mesquita, & Gendron, 2011). Observers perceive targets’ cues, infer their internal states, and respond accordingly (Zaki & Ochsner, 2011). Effective communication between targets and observers in turn facilitates social learning (Olsson et al., 2016), cooperation (Fitzsimons, Finkel, & VanDellen, 2015; Zaki & Williams, 2013), and the formation and maintenance of relationships (Williams, Morelli, Ong, & Zaki, 2018).

Hundreds of studies across the social sciences have examined communication through emotional facial expressions, but virtually all of this work—especially in cognitive neuroscience—focuses exclusively on observers (e.g. Wood et al., 2016). Perceiving emotional facial expressions tends to engage two complimentary sets of brain regions, each broadly associated with distinct social cognitive processes (Zaki & Ochsner, 2012). First, observers vicariously experience emotional states congruent with targets’ facial displays, a process known as *experience sharing*. Experience sharing tracks activity in brain structures associated with visceral and affective states, such as ventral striatum, insula, amygdala, anterior cingulate cortex (ACC), and ventromedial prefrontal cortex (vmPFC; Singer & Klimecki, 2014; Zaki et al., 2016).

Second, observers reason about targets’ internal states, a process known as *mentalizing*. Mentalizing reliably engages brain structures including temporoparietal junction (TPJ), superior temporal sulcus (STS), posterior cingulate cortex (PCC), precuneus, and medial prefrontal cortex (mPFC; Koster-Hale & Saxe, 2013; Schaafsma

et al., 2015). Although they can be dissociated, observers often engage both of these systems when they encounter complex social cues (Redcay et al., 2010; Schilbach et al., 2010).

By contrast, almost no research has examined the brain systems that support targets' *production* of emotional facial displays. Data on the brain basis of producing such expressions could help inform theories of their underlying psychological processes. Traditional theories describe facial expressions as reflexive 'read-outs' of subjective experience (e.g. Ekman, 1972; Buck, 1984). If this is the case, then generating emotional facial expressions should recruit brain structures engaged by experiencing emotion, such as the ventral striatum, insula, amygdala, ACC, and vmPFC (Lindquist et al., 2012; Lindquist et al., 2016). A second theoretical perspective emphasizes that targets might deliberately use facial expressions to influence observers (e.g. Crivelli & Fridlund, 2018; Niedenthal et al., 2010; Martin et al., 2017). Savvy social influence requires mentalizing (Tomasello, 2010), setting up the intriguing prediction that producing affective facial displays might recruit brain regions such as TPJ, STS, PCC, precuneus, and mPFC (Schurz et al., 2014). Targets may thus draw upon brain systems for facial expression that overlap with those employed by observers during facial perception.

Despite recent technological advances, no previous research has directly related measures of brain activity and emotional facial expressions. Several research teams have recorded targets' brain and facial muscle activity by combining fMRI with facial electromyography (EMG). Targets in these studies produced facial EMG responses, and recruited brain structures broadly associated with experiencing emotion and mentalizing, when they viewed emotional images and faces (Heller et al., 2011; 2014; Likowski et al.,

2012; Rymarczyk et al., 2018). Although revealing, this work does not isolate brain activity that “tracks” simultaneous facial movement on a trial-by-trial basis. By isolating brain activity that parametrically tracks EMG activity, here we provide stronger evidence about the neural correlates of facial movement than past work.

Moreover, previous research has not examined the neural correlates of producing facial expressions in the context of emotion communication. This is crucial, because social contexts might fundamentally change the psychological and neural mechanisms associated with producing facial displays. For instance, targets often smile more intensely when viewing pleasant stimuli in the presence of other people (Hess et al., 1995; Jakobs, Manstead, & Fischer, 1999). This evidence suggests that targets “tune” their facial displays in the presence of observers (Bavelas & Chovil, 2000; Van Kleef, 2010), possibly by deliberately taking observers’ perspectives. If social tuning involves perspective taking, targets should engage brain structures associated with mentalizing when they produce facial expressions, especially during communication with observers.

Here, we provide the first examination of the brain systems associated with producing emotional facial expressions during communication. We recruited 16 pairs of friends (total $N = 32$; final $N = 29$) to take turns playing the role of target in the context of an emotional communication task. Participants viewed positive and neutral images and rated their emotional reactions to each image (**Figure 1a**). Throughout the task, participants underwent simultaneous fMRI scanning and EMG recording at the *zygomaticus major* site, a facial muscle associated with smiling. During 50% of trial blocks, participants were told that their friend could see them via video camera and that they should clearly communicate their emotions through facial expressions. During the

other 50% of blocks, participants were told that the video camera was off and that they should respond naturally (**Figure 1b**). This design crossed participants' experience of emotion (positive versus neutral) with the opportunity to convey their feelings to an observer (video camera on versus off).

To identify the neural correlates of producing emotional facial expressions, we developed a novel approach for relating brain activity and facial movements. In addition to examining brain activity across conditions, we also isolated regions in which BOLD parametrically tracked facial EMG responses on an image-by-image basis. Specifically, we combined simultaneous fMRI and facial EMG recording with psychophysiological parametric modulation techniques (see *Data Analysis in Method*). We applied this method to detect brain activity that parametrically tracked facial muscle activity at *zygomaticus major* from trial to trial. This approach allowed us to directly relate participants' brain activity to their facial movements, and to examine brain-facial movement relationships as a function of social and emotional contexts.

Figure 1. Image-viewing (a) trial structure and (b) task structure. On each trial, participants viewed a jittered fixation cross display (2000-12000 ms), followed by a positive or neutral image (3000 ms), and then rated their emotional reaction on a 7-point valence scale (3000 ms). Participants viewed images under the instruction that their facial expressions were visible to a friend via video camera (Video ON) or that the video camera was off (Video OFF).

Results

Valence Ratings

We tested the main effects of viewing positive versus neutral images, and of viewing images with the video camera on versus off, and their interaction and simple effects in a series of mixed effect linear regression models. As predicted, participants rated positive images ($M = 4.98$, $SD = 1.61$) as more pleasant than 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]. Interestingly, image valence also interacted with video recording to predict valence ratings, $b = .19$, $t = 2.55$, $p = .011$, 95% CI [.067, .32]. In particular, participants rated positive images as more pleasant when the video camera was on ($M = 5.03$, $SD = 1.64$) versus off ($M = 4.93$, $SD = 1.58$), $b = .10$, $t = 2.14$, $p = .032$, 95% CI [.0036, .20]. However, participants did not rate neutral images differently as a function of video recording.

Facial Electromyography

We further examined whether image valence and video recording also influenced participants’ facial EMG activity at the *zygomaticus major* site. We tested the main effects of positive versus neutral image-viewing, and of viewing images with the video camera on versus off, and evaluated their interaction and simple effects through mixed effect linear regression models. Participants exhibited greater EMG activity in response to viewing positive ($M = 2.05$, $SD = .30$) versus neutral images ($M = 1.97$, $SD = .27$), $b = .033$, $t = 2.45$, $p = .021$, 95% CI [.016, .056]. Video recording also increased participants’ EMG activity during both positive image-viewing (Video ON: $M = 2.12$, SD

= .31; Video OFF: $M = 1.97$, $SD = .28$), $b = .16$, $t = 6.77$, $p < .001$, 95% CI [.14, .17]; and neutral image-viewing (Video ON: $M = 2.02$, $SD = .28$; Video OFF: $M = 1.92$, $SD = .26$), $b = .096$, $t = 4.67$, $p < .001$, 95% CI [.077, .12]. However, a significant interaction with image valence revealed that video recording increased EMG activity to a greater extent during positive versus neutral image-viewing (**Figure 2a**), $b = .061$, $t = 4.79$, $p < .001$, 95% CI [.037, .085].

Interestingly, while intentionally communicating with observers, participants produced facial expressions that tracked their reported emotional experience more strongly. A series of mixed effect linear regression models revealed that participants' EMG activity tracked their valence ratings when the video camera was on, $b = .029$, $t = 10.87$, $p < .001$, 95% CI [.025, .034]; as well as when the video camera was off, $b = .010$, $t = 3.60$, $p < .001$, 95% CI [.0047, .015]. However, this relationship was significantly stronger with the video camera on versus off (**Figure 2b**), $b = .018$, $t = 6.11$, $p < .001$, 95% CI [.012, .023].

Figure 2. Mean EMG responses by valence and video recording interactions: (a) image valence and (b) valence ratings. Error bars and ribbons depict 95% confidence intervals.

fMRI Results

Univariate contrasts. Univariate analyses tested the influence of image valence and video recording on BOLD activity. When viewing positive versus neutral images (Positive > Neutral), participants exhibited greater activity in right insula and right amygdala (**Figure 3a**), as well as in other regions (**Table 1**). These brain structures are commonly recruited during emotional experiences (Lindquist et al., 2012; Lindquist et al., 2016), and according to Neurosynth meta-analyses, the coordinates of peak activity tracked emotional terms in published neuroimaging research (z 's > 3.91; **Supplementary Table 1**).

When viewing images during video recording (ON > OFF), participants showed greater activity in bilateral temporoparietal junction (TPJ), bilateral posterior superior temporal sulcus (STS), posterior cingulate cortex (PCC), and precuneus (**Figure 3b**), in addition to other regions (**Table 2**). These brain structures are commonly recruited during mentalizing (Schurz et al., 2014) and their activity tracked terms related to mentalizing in Neurosynth meta-analyses (z 's > 3.54; **Supplementary Table 1**).

Critically, and consistent with participants' increased facial EMG activity, both main effect contrasts (Positive > Neutral; ON > OFF) revealed greater activity in regions of sensorimotor cortex including supplementary motor area (SMA) and primary motor, premotor, and primary and secondary somatosensory cortices. These regions contribute to executing motor movements (Grèzes & Decety, 2000) and their activity tracked movement terms on Neurosynth (z 's > 3.80; **Supplementary Table 1**).

Figure 3. 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) with the video camera on (versus off). 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 with the video camera on.

Table 1				
<i>Main effect of image valence: Positive > Neutral.</i>				
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
<i>Note: Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.</i>				

Table 2

Main effect of video recording: ON > OFF.

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: Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.

Brain activity tracking facial movement. We further identified brain regions whose activity parametrically varied with facial EMG activity. To do so, we coded parametric regressors with participants' EMG responses on a trial-by-trial basis, and entered these regressors into general linear models that controlled for potential collinearity with image-viewing by including relevant main effect, interaction, and simple effect regressors whenever EMG regressors spanned multiple task conditions. Researchers have previously used similar techniques to identify the neural correlates of skin conductance responses, muscle reflexes, and non-facial muscle movements (see *Data Analysis in Method*).

Collapsing across all task conditions, EMG activity tracked activity in precuneus and regions of sensorimotor cortex including supplementary motor area (SMA), and right premotor and bilateral primary somatosensory cortices, among other regions (**Table 3**). We next examined the relationship between BOLD and EMG activity for trials where participants viewed positive images, collapsing across video camera on and off conditions. During positive image-viewing, EMG activity tracked greater activity in left ventral striatum (**Figure 3c**), right caudate, left insula, and anterior cingulate cortex (ACC), amongst other regions (**Table 4**). Consistent with previous meta-analyses (Lindquist et al., 2012; Lindquist et al., 2016), these activations tracked emotional terms on Neurosynth (z 's > 4.77 ; **Supplementary Table 2**).

We further examined the relationship between BOLD and EMG activity when participants viewed positive images under the belief that they were visible via video camera. During positive image-viewing with the video camera on, EMG activity tracked increased activity in right temporoparietal junction (TPJ), right anterior superior temporal

sulcus (STS), and precuneus (**Figure 3d**). Following previous meta-analysis (Schurz et al., 2014), these activations tracked terms related to mentalizing on Neurosynth (z 's > 3.88; **Supplementary Table 2**). EMG activity also tracked increased activity in ventral striatum, which tracked the term “monetary reward” on Neurosynth ($z = 4.77$), amongst other regions (**Table 5**). In both contrasts, EMG activity continued to track regions of sensorimotor cortex, and these activations tracked movement terms on Neurosynth (z 's > 3.13; **Supplementary Table 2**).

Table 3				
<i>EMG parametric contrast collapsing across all task conditions.</i>				
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
<i>Note:</i> Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.				

Table 4				
<i>EMG parametric contrast during positive image-viewing.</i>				
Region	Z score	<i>x</i>	<i>y</i>	<i>z</i>
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
<i>Note:</i> Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.				

Table 5				
<i>EMG parametric contrast during positive image-viewing with the video camera on.</i>				
Region	Z score	<i>x</i>	<i>y</i>	<i>z</i>
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
<i>Note:</i> Coordinates are in Montreal Neurologic Institute (MNI) stereotaxic space.				

Discussion

By providing the first direct evidence about the brain basis of generating emotional facial expressions, this study produces multiple novel insights about affect and communication. In particular, we find that while producing emotional facial expressions, participants engaged brain systems similar to those associated with *perceiving* expressions—and that this activity reflected the communicative context under which they produced expressions.

By examining parametrically related time-locked BOLD and facial EMG signals, we found that activity in three key sets of brain structures tracked EMG responses on a trial-to-trial basis. Across all conditions, EMG activity tracked engagement of regions within sensorimotor cortex that contribute to executing motor movements (Grèzes & Decety, 2000). When participants 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 (Lindquist et al., 2012; Lindquist et al., 2016). When participants viewed positive images with the video camera on—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 (Schurz et al., 2014).

In addition to revealing brain correlates of producing emotional facial expressions, these findings synthesize competing views about the nature and social functions of such expressions. Traditional theories of emotion posit that targets' expressions reveal how they experience salient events (e.g. Ekman, 1972; Buck, 1984), such that producing facial expressions should recruit brain systems engaged by experiencing emotion. In contrast, a competing perspective argues that targets'

expressions reveal their attempts to influence observers (e.g. Crivelli & Fridlund, 2018; Niedenthal et al., 2010; Martin et al., 2017), implicating brain systems involved in mentalizing. However, these two perspectives are not mutually exclusive. Previous behavioral research has generated support for both predictions, as targets produce facial expressions in response to emotional stimuli and the presence of other people (Hess et al., 1995; Jakobs, Manstead, & Fischer, 1999). We replicate those findings, and likewise find that producing facial expressions engages brain structures broadly associated with experiencing emotion and mentalizing—in response to viewing positive images, and viewing them while communicating with an observer.

Previous neuroimaging research has generated some support for these predictions but this evidence has faced technological and experimental constraints. Participants have viewed emotional images and faces while undergoing combined fMRI scanning and facial EMG recording (Heller et al., 2011; 2014; Likowski et al., 2012; Rymarczyk et al., 2018). However, technological constraints have previously prevented researchers from directly relating 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. In addition, no prior fMRI research has examined how targets generate facial expressions during live interaction with observers.

The present study addresses these limitations and thus provides the most direct evidence to date of brain systems that support facial expression during communication. First, we experimentally manipulated both the emotions that targets experienced and their goals for communication. This design generated task conditions in which targets conveyed information about their subjective experience through their facial expressions.

Second, we developed a novel method for directly relating measures of brain activity and facial muscle movement. By combining simultaneous fMRI and facial EMG recording with psychophysiological parametric modulation techniques, we identified brain activity that parametrically tracks facial movement on a trial-to-trial basis. This innovation isolates brain activity directly related to producing facial movement from brain activity that responds to task conditions but does not track facial movement. 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 (Schippers et al., 2009; 2010).

This work also generates new insights into how targets facilitate shared understanding with observers. Participants produced EMG activity that tracked their reported experience more strongly during video recording than with the video camera off. In other words, participants produced “clearer” facial expressions when communicating with their friends. This finding suggests that targets may adopt observers’ perspectives, and produce facial expressions that reveal their internal states more accurately, when they wish to be understood (Bavelas & Chovil, 2000; Van Kleef, 2010). This interpretation explains why targets sometimes amplify their facial expressions in social settings (Hess et al., 1995; Jakobs, Manstead, & Fischer, 1999). Such “social tuning” may be a vital form of *interpersonal emotion regulation*—the ways in which individuals manage their own and others’ emotions through social interaction (Zaki & Williams, 2013). Indeed, individuals who openly communicate their feelings develop more supportive relationships and social networks for regulating their emotions (Williams et al., 2018).

Future studies should directly test whether clear facial communication improves the social-emotional functioning of targets, observers, and their relationships.

This research further clarifies the neural mechanisms by which targets communicate with observers. Targets and observers recruit similar brain systems during communication (Schilbach et al., 2010; Schippers et al., 2009). In particular, their brain activity becomes temporally coupled (Hasson et al., 2012) during both verbal (Dikker et al., 2014; Silbert et al., 2014) and non-verbal interaction (Bilek et al., 2015; Schippers et al., 2010), including facial communication (Anders et al., 2011). When viewing and mimicking targets' expressions, observers recruit brain systems broadly associated with mentalizing and experiencing emotion (see Niedenthal et al., 2010 for review). By showing that targets recruit similar systems when producing expressions, this work clarifies how dyads synchronize brain activity related to experiencing emotion (Anders et al., 2011). 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 (Bilek et al., 2015; Schippers et al., 2010). Future work combining simultaneous fMRI and psychophysiological recording could investigate how dyads synchronize their brain activity, facial behavior (e.g. Fischer & Hess, 2017), and peripheral physiology (e.g. Butler, 2015).

Successful cooperation requires clear communication. Affective neuroscience has largely viewed social targets as stimuli, but in fact they are active participants in social exchange, including when they produce facial expressions to deliberately 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.

Method

Participants

We recruited 16 pairs of participants (total $N = 32$) from the Stanford University student body and local community. We ceased data collection once we reached this target sample. All participants were at least 18 years old ($M = 20.44$ years; $SD = 2.76$ years) and they comprised an ethnically diverse sample representative of the Bay Area (31.3% Caucasian). We obtained participants' informed consent in accordance with the Stanford University Research Compliance Office guidelines.

We recruited dyads of close friends given previous evidence that unfamiliar observers can inhibit or fail to influence facial expressions of emotion (Buck et al., 1992; Wagner & Smith, 1991). Within each dyad, both participants first completed an online screening inventory to assess the duration of their friendship, their weekly contact, and the closeness of their relationship via the Inclusion of Other in the Self Scale (IOS; Aron, Aron, & Smollan, 1992). We required that dyads meet the following inclusion criteria: average friendship length of at least 6 months ($M = 20.93$ months; $SD = 14.84$ months), contact at least two times per week ($M = 8.90$ times; $SD = 6.85$ times), and average IOS score of at least 3 ($M = 4.27$; $SD = 1.18$).

See *Analysis* and *Results* for information on participants whose data we excluded due to technical failures and final N s for each analysis.

Stimuli

For the fMRI experiment, we presented positive images that were sourced by our research team and neutral images from the International Affective Picture System (IAPS;

Lang et al., 1999). In an initial pilot study, 10 pilot participants viewed 120 positive and 120 neutral images from IAPS and the Geneva Affective Picture Database (GAPED; Dan-Glauser & Scherer, 2011). Item analyses determined that images of animals and people evoked larger EMG responses at the *zygomaticus major* site than inanimate images, $b = .38$, $t = 10.64$, $p < .001$, 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 the second pilot study, we presented 120 of these positive images and 120 neutral IAPS and GAPED images to 6 new pilot participants. These pilot participants smiled significantly more during positive ($M = 3.52$, $SD = .63$) versus neutral image-viewing ($M = 2.84$, $SD = .57$), as shown by larger EMG responses at the *zygomaticus major* site, $b = .68$, $t = 22.02$, $p < .001$, 95% CI [.62, .74]. Likewise, they reported significantly 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 these positive images for the fMRI experiment and used pilot participants' valence ratings to balance positive images across image blocks.

We presented 120 positive images and 60 neutral IAPS images in the fMRI study. Due to timing constraints, we reduced the experiment to 180 trials total (60 trials per run). We were primarily interested in BOLD signal changes associated with viewing positive images and viewing positive images with the video camera on, rather than viewing neutral images. To maximize statistical power for these parametric contrasts, we therefore included twice as many positive images (120) as neutral images (60).

Procedure and Design

Participants completed three 10-minute runs (60 trials each) of positive and neutral image-viewing while undergoing simultaneous facial EMG recording and fMRI scanning. 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). Each run included two blocks of images and each block was assigned to one of two video recording 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 at the top of the screen displaying the words ‘VIDEO ON’ adjacent to a red circle (adapted from Somerville et al., 2013). Participants were further led to believe that their friends would later review these video recordings and try to accurately rate the emotions participants experienced. We therefore instructed participants to clearly communicate their emotions through facial expressions when the video camera was on. 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 with the video camera off. 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 prior to beginning the main task. In actuality, participants were not video recorded at any point.

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 with respect to

image valence and IAPS images were additionally balanced for arousal and animacy. To control for block order effects, we randomized block presentation order across participants. Within each block, we pseudo-randomized image presentation order and jitter duration to optimize statistical power for fMRI analyses. Specifically, we used the `optseq2` program to generate six different optimized image valence/jitter sequences and we randomly assigned these sequences to the six image blocks for each participant (Dale, 1999; Dale, Greve & Burock, 1999). These sequences preset the order in which participants viewed images with positive or neutral valence within each image block. However, we randomized *which* positive or neutral image participants viewed on a given trial.

We further randomized the six image blocks and six image valence/jitter sequences across the two video conditions such that participants viewed three blocks of images under each video condition. To control for video condition order effects, we further counterbalanced video condition order across participants. In particular, we generated six possible video condition orders that ensured (1) participants viewed one image block with the video camera on and one image block with the video camera off during each run, (2) participants never viewed more than two consecutive image blocks under the same video condition, and (3) participants never completed more than two runs of image-viewing with the same video condition order.

Following the main experiment, participants underwent an anatomical fMRI scan. After scanning, participants were fully debriefed about the purpose of the experiment.

Data Acquisition and Processing

Facial electromyography. We recorded facial muscle activity throughout the experiment via facial electromyography (EMG) at the left *zygomaticus major* site, a facial muscle associated with smiling and positive emotional experience (see Dimberg, 1990). To reduce signal impedances, we cleaned skin sites with alcohol pads, abraded with NuPrep, and washed with water. We then adhered 11-mm BioPac Ag/AgCl radiotranslucent electrode pairs in accordance with Fridlund and Cacioppo's (1986) guidelines.

EMG responses were recorded and amplified with a BioPac MP150 Data Acquisition System equipped with a BioPac EMG100C-MRI Electromyogram Amplifier, which reduces EPI-induced magnetic gradient switching artifact by approximately 100x (40 dB) compared to typical amplifiers. EMG activity was sampled at a rate of 1,000 Hz with a gain of 1,000 Hz, hardware low and high pass filtered at 500 and 10 Hz, and notch filtered at 60 Hz. EMG recordings were further processed with the Autonomic Nervous System Laboratory (ANSLab v2.4, Wilhelm & Peyck, 2005) and custom Matlab scripts (The Mathworks, Natick, MA). EMG data were high pass filtered at 28 Hz (van Boxtel, 2001), comb band filtered at 60 Hz, resampled at 10 Hz, rectified, and smoothed. This high-pass filter further minimized electromagnetic noise generated by EPI slice acquisition at 23 Hz (46 slices per 2-second TR).

We calculated trial-by-trial pre-stimulus proximal baseline (1000 ms) and stimulus presentation (2000 ms) averages. We then deducted proximal baseline averages from stimulus presentation averages to generate baseline-corrected difference scores (in μV). For facial electromyography analyses, we log-transformed difference scores to

correct for skewness typical of EMG.

Neuroimaging. We collected 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; 80×80 matrix; flip angle 90° ; FOV $23.2 \times 23.2 \text{ cm}$). Following the three functional scans, we collected a high-resolution T1-weighted anatomical scan (186 axial slices of 0.9 mm^3 voxels; TR = 7.2 ms; TE = 2.8 ms; 256×256 matrix; flip angle 12° ; FOV $25.6 \times 23.2 \text{ cm}$).

MRI data were preprocessed and analyzed in FSL (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012). To ensure T-1 stabilization, the first 4 TRs (i.e. the length of the first trial) were deleted. 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 (100s 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). Each functional scan was analyzed through a series of mixed effect general linear models (GLMs). We convolved regressors with a canonical gamma hemodynamic response function (lag $M = 6 \text{ s}$, $SD = 3 \text{ s}$) and applied temporal filtering. All GLMs used FILM prewhitening and included confound regressors for temporal derivatives, standard motion parameters, and motion outliers.

We subsequently ran second-level analyses over each participant's three first-level analyses and group-level analyses (FLAME 1) over second-level analyses. We then applied stringent parametric corrections to correct for multiple comparisons (Eklund, Nichols, & Knutsson, 2016). Specifically, we used a cluster-defining threshold of $z >$

3.09 ($p < .001$) with FWE correction ($p < .05$).

Data Analysis

Missing cases. One participant's fMRI data failed to record due to instrument failure.

Two participants failed to respond to more than 20% of total trials. We excluded these three participants' data from all analyses (final $N = 29$).

Behavioral data. As a manipulation check, we first confirmed that participants responded to image valence and video camera manipulations as predicted. With respect to image valence, we tested whether participants reported more positive experience and smiled more while viewing positive versus neutral images. To evaluate the video camera manipulation, we further examined whether participants smiled more with the video camera on than off. Specifically, we conducted mixed effect linear regression analyses to evaluate these main effects over participants' valence ratings and log-transformed EMG difference scores.

For the main behavioral analyses, we tested whether being visible to a friend influenced participants' experience or expression of positive affect. We therefore tested whether image valence interacted with video camera condition to influence participants' reported experience and facial expressivity. To test for this interaction, we ran mixed effect linear regression models over valence ratings and log-transformed EMG difference scores. Follow-up mixed effect linear regression analyses examined the simple contrasts between conditions.

We further evaluated whether being visible to a friend influenced how strongly participants' facial expressions tracked their reported experience. A mixed effect linear

regression analysis therefore tested the interaction between participants' valence ratings and video camera condition for their log-transformed EMG difference scores. Follow-up mixed effect linear regression models assessed the simple effect of valence ratings with the video camera either on or off.

Individual differences in participants' mean response tendencies, and the slopes of their responses to image valence, significantly improved model fit as random effects and were included in all models. Participants' response slopes to video camera condition were also included as random effects in all facial EMG analyses because they further improved model fit. We obtained 95% confidence intervals for all analyses by conducting follow-up bootstrapped regression analyses using 1,000 iterations (Preacher & Hayes, 2004).

BOLD data. A series of manipulation checks ensured that the image valence and video condition manipulations influenced neural activity as expected. A general linear model evaluated the main effects of image valence (Positive > Neutral) and video camera condition (ON > OFF). To ensure that image valence and video camera regressors reflected main effects only, we also included a regressor coding their interaction. This control effectively removed any variance shared between the interaction and main effect regressors. To relate EMG and BOLD signals, we conducted general linear models with parametric regressors reflecting participants' trial-by-trial EMG difference scores (Critchley, et al., 2000; 2002; Neuner et al., 2010; Van Rootselaar et al., 2007). As a manipulation check, we first confirmed that EMG responses tracked activity within sensorimotor cortex across task conditions. We next examined how EMG responsivity tracked brain activity within particular conditions. Specifically, we generated two

separate physiological regressors spanning positive image-viewing and positive image-viewing with the video camera on. These regressors revealed brain activity tracking participants' EMG responses in response to (1) experiencing emotion and (2) communicating those experiences.

Critically, we controlled for potential collinearity with BOLD responses to image-viewing in two ways. First, to eliminate collinearity with the image-viewing task, we demeaned EMG regressors for each run (Mumford, Poline, & Poldrack, 2015). Second, to control for collinearity with task manipulations, we included relevant task contrast regressors whenever EMG regressors spanned more than one task condition. Specifically, we included main effect and interaction regressors when examining EMG overall and simple 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 (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011).

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. J.Z. contributed to study design and manuscript preparation.

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Supplementary Table 1		
<i>Neurosynth terms associated with brain activity: Univariate contrasts.</i>		
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
Video recording (ON > OFF)	---	---
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 2		
<i>Neurosynth terms associated with brain activity: EMG parametric contrasts.</i>		
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 with video camera on	---	---
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