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Automatic facial reactions to facial, body, and vocal expressions: A stimulus-response compatibility study

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Abstract
When perceiving emotional facial expressions there is an automatic tendency to react with a matching facial expression. A classic explanation of this phenomenon, termed the matched motor hypothesis, highlights the importance of topographic matching, that is, the correspondence in body parts, between perceived and produced actions. More recent studies using mimicry paradigms have challenged this classic account, producing ample evidence against the matched motor hypothesis. However, research using stimulus-response compatibility (SRC) paradigms usually assumed the effect relies on topographic matching. While mimicry and SRC share some characteristics, critical differences between the paradigms suggest conclusions cannot be simply transferred from one to another. Thus, our aim in the present study was to directly test the matched motor hypothesis using SRC. Specifically, we investigated whether observing emotional body postures or hearing emotional vocalizations produces a tendency to respond with one's face, despite completely different motor actions being involved. In three SRC experiments, participants were required to either smile or frown in response to a color cue, presented concurrently with stimuli of happy and angry facial (experiment 1), body (experiment 2), or vocal (experiment 3) expressions. Reaction times were measured using facial EMG. Whether presenting facial, body, or vocal expressions, we found faster responses in compatible, compared to incompatible trials. These results demonstrate that the SRC effect of emotional expressions does not require topographic matching. Our findings question interpretations of previous research and suggest further examination of the matched motor hypothesis.

KEYWORDS
automatic processes, EMG, emotional expressions, stimulus-response compatibility

1 | INTRODUCTION

When perceiving emotional facial expressions there is an automatic tendency to react with a matching facial expression, such as a smile when observing a happy expression or a frown[1] when observing an angry expression. It has been suggested that this tendency to facially match emotional expressions contributes to emotional perception (Neal & Chartrand, 2011; Niedenthal, Mermillod, Maringer, & Hess, 2010; Wood, Rychlowska, Korb, & Niedenthal, 2016) as well as to emotional contagion and empathy (Prochazkova & Kret, 2017; Singer & Lamm, 2009; Sonnby-Borgström, 2002) and both affects and is affected by social relationships (Hess & Fischer, 2014). However, despite its supposed importance for social cognition, the mechanisms behind it are still unclear (Fischer & Hess, 2017; Kozlik, Neumann, &

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[1] English definitions of the word Frown vary. Here and throughout the article, we use it to refer to bringing the eyebrows together, as in the stereotypical expression of anger.

Lozo, 2015; Kraaijenvanger, Hofman, & Bos, 2017; Ramsey, 2018).

In a classic approach to explaining this phenomenon, researchers have often referred to theories of common coding of perception and action (Chartrand, Maddux, & Lakin, 2005; Otte, Habel, Schulte-Rüther, Konrad, & Koch, 2011; Otte, Jost, Habel, & Koch, 2011), relating it to the mirror neuron system (MNS; Chechko, Pagel, Otte, Koch, & Habel, 2016; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006; Press, Richardson, & Bird, 2010; Schulte-Rüther et al., 2017) or to basic motor mimicry (Lee, Dolan, & Critchley, 2008; Otte, Habel, et al., 2011; Wild, Erb, Eyb, Bartels, & Grodd, 2003). In all those different formulations, jointly termed by Hess and Fischer (2013) the *matched motor hypothesis*, the defining feature seems to be the *topographic matching*, that is, the correspondence in body parts, between perceived and produced actions. This explanation is the focus of this research.

In the rest of the introduction, we will start by shortly reviewing how this explanation was treated by two, almost separate, bodies of literature: one using the emotional mimicry paradigm and the other using stimulus-response compatibility. We will then highlight some discrepancies between the paradigms and, finally, outline the current research.

1.1 | Emotional mimicry

The tendency to match facial expressions is commonly measured using *emotional mimicry* (Hess & Fischer, 2013). In this paradigm, participants passively view facial expressions, while their spontaneous facial muscle activity is recorded, often using electromyography (EMG; e.g., Beall, Moody, McIntosh, Hepburn, & Reed, 2008; Dijk, Fischer, Morina, van Eeuwijk, & van Kleef, 2018; Dimberg, 1982; Dimberg, Thunberg, & Elmehed, 2000; Geangu, Quadrelli, Conte, Croci, & Turati, 2016; Rymarczyk, Żurawski, Jankowiak-Siuda, & Szatkowska, 2018). Using this paradigm it was shown that the mere observation of facial expressions produces subtle activations in the observer's corresponding facial muscles (Dimberg, 1982). Thus, for example, passively viewing a smiling face slightly increases the activation in the zygomatic muscle, which pulls up the corners of the mouth.

Mimicry effects are considered automatic. They cannot be suppressed by instruction (Dimberg, Thunberg, & Grunedal, 2002; Korb, Grandjean, & Scherer, 2010) and they are evoked even when stimuli are presented outside of conscious awareness (Dimberg et al., 2000; Kaiser, Davey, Parkhouse, Meeres, & Scott, 2016; Tamietto et al., 2009). The similarities between perceived and automatically evoked behavior, is at the heart of the matched motor hypothesis, leading some researchers to suggest that it results from a direct link between perception and action (Chartrand et al., 2005). More support for this view came from fMRI studies that showed that emotional mimicry is associated with activations in brain areas, such as the inferior frontal gyrus (IFG) and the supplemental motor area (SMA), that are related to the MNS (Likowski et al., 2012; Rymarczyk et al., 2018).

In contrast to this classic approach, accumulating evidence has mounted against the matched motor hypothesis (Hess & Fischer, 2013). First, mimicry studies that included expressions of emotions other than happiness and anger failed to find the same specificity in matching the observed expression. For example, the frontalis muscle that raises the brows was not consistently found in response to expressions of fear. Similarly, mixed results were found in the activation of the levator labii muscle that wrinkles the nose in response to expressions of disgust (see Hess & Fischer, 2013 for a review). Thus, observing facial expressions of fear and disgust does not seem to cause matching of identical motor actions.

Second, emotionally congruent facial expressions were also found in response to observed emotional body postures without a face (Magnée, Stekelenburg, Kemner, & de Gelder, 2007; Tamietto et al., 2009). Similarly, facial reactions were observed when participants listened to emotional vocalizations (Hawk, Fischer, & Van Kleef, 2012; Hietanen, Surakka, & Linnankoski, 1998; Sestito et al., 2013). Thus, emotional expressions evoke congruent facial reactions even without perceiving any facial expression, a finding at odds with a matched motor account.

Third, emotional facial reactions were sometimes found even to neutral faces. In one study, Hess, Houde, and Fischer found such reactions when they told participants the person in the neutral picture was feeling either happy or sad and asked them to judge the intensity of that feeling (Hess, Houde, & Fischer, 2014). In another study, Aguado et al. first showed participants facial stimuli changing from neutral to either happy or angry. Participants that matched the emotional expression while watching this sequence also responded with the same expression later while observing only the neutral face (Aguado et al., 2013). So, when the emotion can be learned from other sources even neutral faces can induce emotional facial reactions.

Thus, in studies using the emotional mimicry paradigm, evidence has accumulated against the matched motor hypothesis. Our aim in the present study was to extend these findings using a new methodology—the stimulus-response compatibility (SRC) paradigm.

1.2 | Stimulus-response compatibility

In a typical experiment using SRC of emotional expressions, participants are asked to quickly respond to a neutral cue (e.g., color) with either a smile or a frown. Critically, the cue is presented concurrently with a task-irrelevant stimulus depicting either a happy or an angry facial expression that can be either compatible or incompatible with the instructed expression. The central finding is that reaction times (RT), measured using facial EMG, are slower for incompatible, compared to compatible trials (i.e., SRC effect; Lee et al., 2008; Otte, Habel, et al., 2011; Wild et al., 2003). Similar to emotional mimicry, the SRC paradigm has been used to study the tendency to match emotional expressions. However, unlike the more recent accounts in mimicry research, studies using SRC tended to stress the importance of topographic compatibility.

The SRC effect is automatic, in that it is unintentional and unavoidable (Heyes, 2011; Schneider & Shiffrin, 1977). As the paradigm requires a response only to the neutral cue, the observed facial expression is completely task irrelevant. Moreover, participants are asked to respond as quickly and as accurately as possible to the neutral cue, thus, being affected by the emotional stimulus is actually task impeding. In some studies, the irrelevant stimulus is presented in a different location (Kozlik & Neumann, 2017) or a different modality (Lee et al., 2008) than the cue, so participants should not even attend to the irrelevant stimulus. Thus, stimuli that are task irrelevant, task impeding and to be ignored nonetheless affected task performance. Even in experiments that did not involve action selection (smile or frown) but had only one prespecified response (e.g., frown), RT were still affected by the observed expressions (Dimberg et al., 2002; Korb et al., 2010; Lee et al., 2008; Otte, Habel, et al., 2011; Press et al., 2010; Wild et al., 2003), further demonstrating the automaticity of the effect. As in the classic mimicry studies, the apparent matching between observed and executed behavior, together with the automatic nature of the effect, were often used as support for a motor matching explanation (Lee et al., 2008; Otte, Habel, et al., 2011; Wild et al., 2003).

This facial SRC effect is similar to the effect obtained with nonemotional actions, such as hand movements, often termed *automatic imitation* (Heyes, 2011). In a classic experiment (Brass, Bekkering, Wohlschläger, & Prinz, 2000) participants were asked to lift either their index finger or their middle finger in response to a number cue, while observing a hand on the screen performing the same action (compatible trials), the opposite action (incompatible trials), or no action at all (baseline trials). They found that compared to baseline, compatible trials were faster and incompatible trials were slower, suggesting that observed actions can both facilitate and interfere with executed actions. These effects were replicated with numerous types of actions, involving hands, fingers, legs, and mouth (for reviews see: Cracco et al., 2018; Heyes, 2011).

Automatic imitation is thought to rely on topographic compatibility (Cracco et al., 2018; Heyes, 2011), as it was shown that it cannot be reduced to spatial compatibility, movement compatibility, or emulation (i.e., the effect of object presentation on action tendency). It is also believed to be dependent on the MNS (Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2011). This view was supported by the finding that disruptive transcranial magnetic stimulation (TMS) of the IFG interferes with automatic imitation of hand movements (Catmur, Walsh, & Heyes, 2009; Newman-Norlund, Ondobaka, van Schie, van Elswijk, & Bekkering, 2010).

Many researchers treated the SRC effect of emotional expressions as just a special case of automatic imitation, thus, assuming that both rely on topographic compatibility and the MNS (Chechko et al., 2016; Otte, Habel, et al., 2011; Press et al., 2010; Schulte-Rüther et al., 2017). Indeed, fMRI studies found that the SRC effect of emotional expressions correlated with brain activations in areas related to the MNS like the IFG and the SMA (Lee et al., 2008; Wild et al., 2003).

To the best of our knowledge, there were no studies directly contradicting the motor matching explanation using SRC of emotional expressions. However, related phenomena provide some clues in this direction. For example, nonemotional facial actions, like opening or closing the mouth, show an SRC effect for observing similar actions performed with a different effector (Leighton & Heyes, 2010; Maister & Tsakiris, 2016). Leighton and Heyes (2010) asked participants to either open or close their hand or their mouth while observing stimuli involving the same kind of actions, that could be either compatible or incompatible, both in the type of movement and in the effector used. Importantly, they found that observing a hand opening or closing affected the speed of mouth opening or closing. These findings suggest that, at least for nonemotional facial actions, movement compatibility, not just effector compatibility, can create the effect.

1.3 | Emotional mimicry versus SRC

As reviewed above, SRC research heavily relied on the automatic imitation literature and tended to favor the motor explanation, while recent mimicry research produced ample evidence against the matched motor hypothesis. However, conclusions cannot be simply transferred from one paradigm to another. While the two paradigms are supposed to tap the same phenomenon, considerable differences can be noted. First, the two paradigms yielded contradicting results in clinical populations. Studies that used mimicry paradigms found significant differences between individuals with autism spectrum conditions and typically developing controls (Beall et al., 2008; McIntosh et al., 2006; Stel, van den Heuvel, & Smeets, 2008) and a similar effect was found in schizophrenia (Varcin, Bailey, & Henry, 2010). However, SRC studies found that the two groups exhibited SRC effects that were not different than controls (Chechko et al., 2016; Press et al., 2010; Schulte-Rüther et al., 2017).

Second, differences were found between other related paradigms. For example, automatic imitation of hand movements, that is thought to be related to facial SRC,

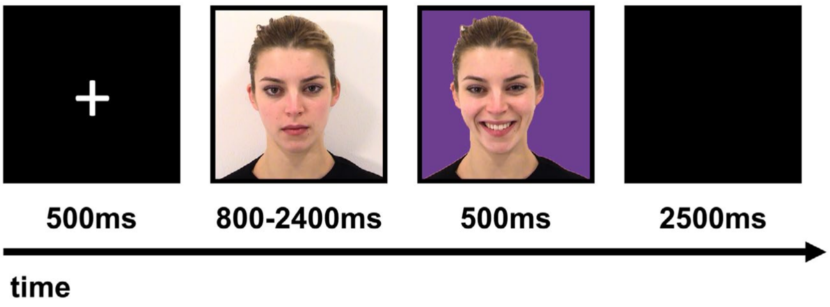

FIGURE 1 The time course of a single trial in experiment 1. A trial started with 500 ms of fixation. Then, a picture presenting a neutral facial expression appeared for either 800, 1,600, or 2,400 ms, followed by a picture of the same actor with an emotional facial expression (here, a happy one) and with the background colored in orange or purple. The trial ended with 2,500 ms of a black screen

was abolished by subliminal presentation (Mele, Mattiassi, & Urgesi, 2014). This contrasts with findings in mimicry studies showing that mimicry can occur even when stimuli are presented outside of conscious awareness (Dimberg et al., 2000; Kaiser et al., 2016; Tamietto et al., 2009). Another related paradigm is *behavioral mimicry*, the copying of behaviors such as face touching or foot tapping (Chartrand & Bargh, 1999), that is thought to be closely related to emotional mimicry (Chartrand et al., 2005). It was shown that behavioral mimicry did not correlate with automatic imitation (Genschow et al., 2017) and a recent review concluded that there is insufficient evidence for drawing parallels between automatic imitation and behavioral mimicry (Ramsey, 2018).

To the best of our knowledge, SRC of emotional expressions was never directly compared to emotional mimicry, but the evidence mentioned above suggests it cannot be safely assumed that they measure the exact same phenomenon. Nonetheless, the SRC effect is often used as a marker of automatic mimicry or MNS activation (Chechko et al., 2016; Press et al., 2010; Schulte-Rüther et al., 2017). Used with special populations, such as people with autism spectrum conditions and schizophrenia, performance that was comparable to controls was taken as evidence for intact mimicry or an intact MNS. Therefore, it is extremely important to gain a better understanding of the underlying mechanism. Since conclusions cannot be safely drawn from mimicry research, it is critical to investigate the motor hypothesis directly using an SRC paradigm.

1.4 | The current research

The current study, therefore, sought to test whether motor matching of observed and executed behavior (topographic compatibility) is necessary for the SRC effect of emotional expressions. Specifically, we investigated facial reactions to emotional vocalizations and body postures. Following previous mimicry studies (Hawk et al., 2012; Hietanen et al., 1998; Magnée et al., 2007; Sestito et al., 2013; Tamietto et al., 2009), we hypothesized that hearing emotional vocalizations or observing body postures that did not include a face, will nevertheless elicit facial SRC effects.

Experiment 1 aimed to conceptually replicate the known finding of facial SRC effect to facial expressions. Experiments 2 and 3 were designed to test our main hypothesis of facial SRC effect to emotional vocalizations and body postures. Keeping the same design as in experiment 1, in experiment 2 we replaced the stimuli of emotional facial expressions with emotional body postures; experiment 3 repeated the same design with emotional vocalizations, thus, allowing us to test the importance of topographic compatibility for the facial SRC effect.

2 | EXPERIMENT 1

Participants' task was to either smile or frown, as quickly as possible, in response to a color cue, superimposed on pictures of actors smiling or frowning (See Figure 1). In some trials, the action in the picture was response-compatible (e.g., a smiling response was made in the presence of a smiling stimulus), while in others it was response-incompatible (e.g., a smiling response was made in the presence of a frowning stimulus). In both cases, the presented expression was irrelevant to the task. RT for frowning and smiling were measured using EMG from the corrugator and zygomatic muscles, respectively. We predicted that, as in previous studies (Lee et al., 2008; Otte, Habel, et al., 2011; Wild et al., 2003), facial RT will be longer when viewing an incompatible expression, compared to a compatible one.

2.1 | Method

2.1.1 | Participants

Participants were 14 students (three males) ages 19–29 years (*M* = 23.71 years, *SD* = 2.81) from the Hebrew University of Jerusalem. All participants gave written informed consent and were either paid an amount equivalent to $10 or received course credit for their participation.

2.1.2 | Materials

Sixty-four still images of actors (half male, half female) portraying a neutral, happy, or angry facial expression were used. We chose still images, rather than video clips, to control the exact timing the emotional expression was displayed. The pictures were extracted from 32 videos from the Amsterdam Dynamic Facial Expression Set (ADFES; van der Schalk, Hawk, Fischer, & Doosje, 2011) of actors changing their expression from a neutral to an emotional one. A pilot study confirmed that the selected videos were highly recognizable (90% mean recognition rate). Images were extracted from the videos, rather than taken from the ADFES stills set, to help creating an illusion of motion when the emotional image followed the neutral one. The background of the emotional images was colored orange in one version, and purple in another.

2.1.3 | Procedure

Figure 1 presents the time course of a single trial. Each trial started with a fixation cross appearing for 500 ms, followed by a picture of a male or female actor performing a neutral expression. The duration of the neutral stimulus varied randomly between 800, 1,600, and 2,400 ms. Then, the neutral picture was replaced by either a happy or an angry picture of the same actor for 500 ms. We had a neutral picture precede the emotional one, as this sequence created an apparent motion illusion, giving the impression that the face was changing from neutral to emotional. The neutral picture was taken from the same video as the emotional picture that followed, which also allowed for a baseline that closely resembled the critical stimulus. The background of the emotional picture was either colored orange or purple and participants' task was to either smile or frown, as quickly as possible, in response to the color. The instructions either read "smile, as you do when you are happy" or "contract your eyebrows, as you do when you are angry." Whether to smile to orange and frown to purple or vice versa was counterbalanced across participants. The trial ended with 2,500 ms of a black screen.

Stimulus presentation was controlled by a PC running E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). We presented four experimental blocks of 40 trials each. Trials consisted of either a happy or an angry stimulus of either a female or a male actor and with the task to either smile or frown. Each block consisted of five trials from each of these eight options, with the order and specific stimuli randomly selected. Prior to the experimental blocks, participants performed a practice block comprising 24 trials, three of each type.

Facial EMG activity was recorded using a BIOSEMI Active-Two amplifier system (BioSemi Biomedical Instrumentation, Amsterdam, the Netherlands) with a sampling rate of 2,048 Hz. Four flat-type active electrodes were placed bipolarly over the left (Dimberg & Petterson, 2000) zygomatic and corrugator muscles, following the guidelines set forth by Fridlund and Cacioppo (1986). The common mode sense (CMS) active electrode and the driven right leg (DRL) passive electrode (http://www.biosemi.com/faq/cms&drl.htm) were attached to the bridge of the nose and right below the hair line, respectively.

2.1.4 | Design

A 2 × 2 within-subject design was used, with task (smile vs. frown) and stimulus compatibility (compatible vs. incompatible) as independent variables. Reaction time, measured as the latency of EMG onset, was the dependent variable.

2.1.5 | Power

Power analysis was conducted using GLIMMPSE software (Kreidler et al., 2013), based on the data reported in Lee et al. (2008). Population effect sizes were not available from this article, as their statistical analysis focused on an extreme subsample of their participants. However, they did report means and standard deviations for the entire sample. GLIMMPSE software allows to estimate sample sizes based on means, SDs, and the correlation between repeated samples. Since correlations were not reported in this article, we used their reported means and standard deviations with a correlation of 0 (most strict). Using these parameters in a repeated measures design indicated that a sample size of 11 should be sufficient to detect the effect with alpha level of 0.05 and power of 0.8.

2.1.6 | Data analysis

EMG data were analyzed offline using BrainVision Analyzer 2.0.4 (Brain Products, Gilching, Germany). After calculating bipolar channels, data were 50–500 Hz band-pass filtered and full-wave rectified. The signal was then smoothed using a 10 Hz low-pass filter. To determine muscle reaction time, EMG onset latency was detected for each trial and each muscle using the EMG Onset Search method implemented in BrainVision Analyzer. For this procedure, the 500 ms prior to the color cue were used as a baseline. EMG onset was searched within the first 2,000 ms following the cue and

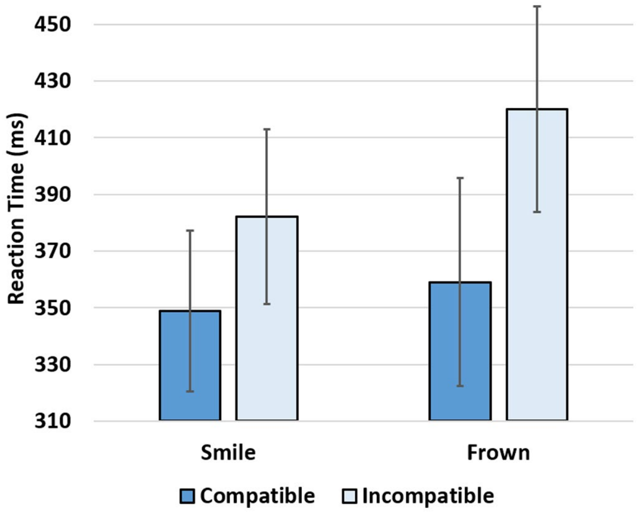

FIGURE 2 RT as a function of compatibility and task in experiment 1. RT were faster in compatible, compared to incompatible trials and more so for frowning compared to smiling. Error bars represent standard errors of the means

had to exceed a threshold of 10 standard deviations from the baseline mean.

Trials were considered correct if we identified an EMG response in the muscle indicated by the cue and only in this muscle. A response was considered reliable if RT were between 100 and 1,000 ms. Incorrect or unreliable trials were excluded from the reaction time analysis and included in a separate error analysis (see Supporting Information). RT were analyzed using repeated measures ANOVA, with task and compatibility as within-subject factors.

The internal consistency of the task was assessed using split-half reliability. Pearson correlation was calculated between the first half of the task (blocks 1–2) and the second half (blocks 3–4). This correlation was calculated separately for each muscle and condition.

2.2 | Results

On average, participants responded correctly and reliably on 73% of the trials[2] ($SD = 11.58$). The internal consistency of the task, as indicated by a split-half reliability, was high (See Table S1 in the Supporting Information). Average RT are presented in Figure 2 and average time courses of the EMG response are presented in Figure S1 in the Supporting Information. As predicted, the results of the repeated measures ANOVA indicated that RT were faster in compatible, compared to incompatible trials, $F(1,13) = 23.96$, $p < .001$, $\eta_p^2 = 0.648$. While the main effect of task was not significant ($p > .05$), the interaction between compatibility and task indicated that the compatibility effect was more pronounced for frowning compared to smiling, $F(1,13) = 5.30$, $p = .039$, $\eta_p^2 = 0.289$. Participants also had more errors in incompatible trials, responding more with the opposite muscle or with both muscles (for a detailed error analysis, see Supporting Information).

2.3 | Discussion

As expected, RT for smiling and frowning were faster when observing compatible, compared to incompatible facial expressions. With these findings, we replicate previous studies showing an SRC effect for emotional facial expressions (Lee et al., 2008; Otte, Habel, et al., 2011; Wild et al., 2003). Our next step was to test whether this effect relies on topographic compatibility.

3 | EXPERIMENT 2

In experiment 2, we explored whether facial SRC to emotional expressions depends on topographic compatibility. Specifically, we asked whether facial SRC would be produced in response to emotional body postures. The paradigm was similar to experiment 1, except that here, the pictures were of angry or happy body postures (See Figure 3). We predicted that although the executed actions (facial expressions) were not topographically compatible with the observed actions (body postures), RT will still be longer when viewing an incompatible stimulus, compared to a compatible one.

3.1 | Method

3.1.1 | Participants

Participants were 28 students (four males) ages 20–31 years ($M = 23.86$ years, $SD = 2.48$) from the Hebrew University of Jerusalem. All gave written informed consent and were either paid an amount equivalent to $10 or received course credit for their participation.

3.1.2 | Materials

Instead of the face stimuli used in experiment 1, we used here emotional body stimuli. Sixty-three still images of actors (half male, half female) performing a neutral, happy, or angry body

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[2] The rate of correct and reliable trials was consistent across our three experiments, though it was somewhat lower than in previous studies using facial SRC. However, tasks and analyses vary. Studies that used a similar paradigm also had comparable rates of correct and reliable trials (Chechko et al., 2016; Otte, Habel, et al., 2011; experiment 1). Also note that we chose to use rather stringent criteria, both for reliability and for determining EMG onset, which may have also affected our results.

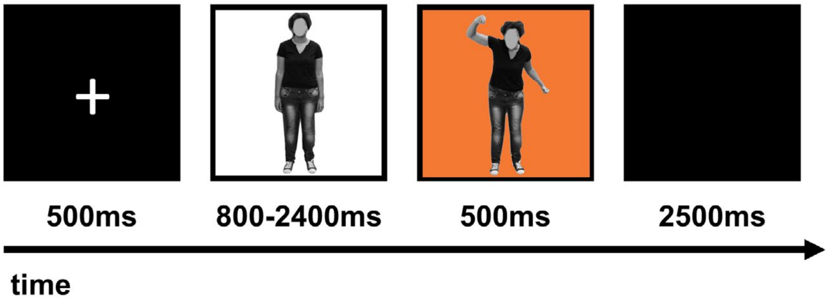

FIGURE 3 The time course of a single trial in experiment 2. A trial started with 500 ms of fixation. Then, a picture presenting a neutral body posture appeared for either 800, 1,600, or 2,400 ms, followed by a picture of the same actor with an emotional posture (here, an angry one) and with the background colored in orange or purple. The trial ended with 2,500 ms of a black screen

expression were used. The pictures were taken from the standardized and validated Bochum Emotional Stimulus Set (BESST; Thoma, Bauser, & Suchan, 2013). All the chosen pictures were highly recognizable (97% mean correct categorization) based on the validation data provided with the BESST set. Some of the images were resized so that the neutral and emotional pictures of the same actor were comparable. This was done to increase the illusion of motion in the trial's sequence of neutral and emotional stimuli. The background of the emotional images was colored orange in one version, and purple in another.

3.1.3 | Design, procedure, and data analysis

The design, procedure, and data analysis were identical to those used in experiment 1 (See Figure 3 for a trial outline).

3.1.4 | Power

In experiment 1, using an identical design, number of trials and analysis, 14 participants were enough to detect and replicate the facial SRC effect. However, experiment 2 explored a novel effect, namely, facial SRC to body stimuli. As it was difficult to anticipate the effect size and correlation, proper calculation of sample size was not possible. Thus, to allow for a potentially smaller effect size, we decided to double the number of participants we would have used for faces.

3.2 | Results

On average, participants responded correctly and reliably on 75% of the trials (*SD* = 13.54). As before, only correct and reliable trials were used in the analysis. One participant was excluded entirely because of an exceptionally low percent of correct and reliable trials (<50%).

The internal consistency of the task, as indicated by a split-half reliability, was high (See Table S1 in the Supporting Information). Average RT are presented in Figure 4 and average time courses of the EMG response are presented in Figure S2 in the Supporting Information. The results of the repeated measures ANOVA indicated that, as predicted, RT were faster in compatible, compared to incompatible trials, $F(1,26) = 15.76$, $p = .001$, $\eta_p^2 = 0.377$. The effects of task and the interaction were not significant ($p > .05$). Error analysis indicated more responses with both muscles in incompatible, compared to compatible trials (see Supporting Information).

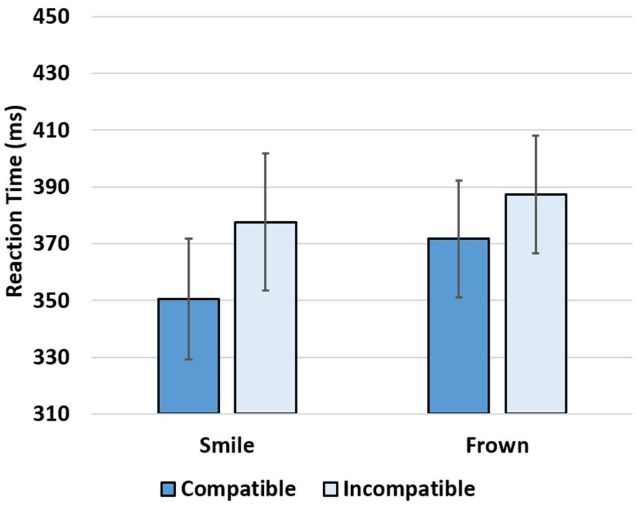

FIGURE 4 RT as a function of compatibility and task in experiment 2. RT were faster in compatible, compared to incompatible trials. Error bars represent standard errors of the means

3.3 | Discussion

In experiment 2, executed and observed actions were no longer topographically compatible. While they were sometimes compatible in the emotion they expressed, the actions themselves always involved completely different body parts. Nonetheless, an SRC effect emerged, with RT significantly shorter for compatible, compared to incompatible trials. These findings demonstrate that topographic compatibility is not necessary for producing automatic facial responses to emotional expressions using the SRC method.

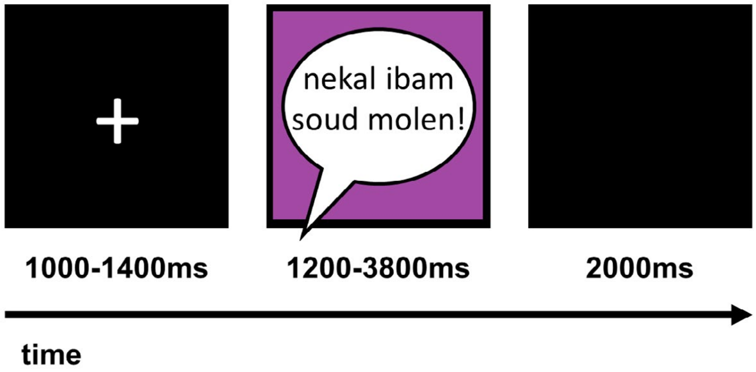

FIGURE 5 The time course of a single trial in experiment 3. A trial started with a fixation cross, appearing for either 1,000, 1,200, or 1,400 ms. Then, an emotional stimulus was played, and the screen changed to either green or purple. The trial ended with a 2,000 ms black screen

4 | EXPERIMENT 3

Next, we wanted to extend the previous results to the auditory modality. Experiment 3 utilized the same paradigm, but instead of a visual emotional stimulus, synchronized the color cue with an auditory stimulus of happy or angry vocal expressions (See Figure 5). Although producing emotional vocalizations requires different motor actions than producing a facial expression, we expected facial reactions to still be faster in emotionally congruent trials compared to incongruent ones.

4.1 | Method

4.1.1 | Participants

Participants were 24 students (seven males) ages 18–34 years ($M = 23.42$ years, $SD = 3.79$) from the Hebrew University of Jerusalem. All gave written informed consent and were either paid an amount equivalent to $10 or received course credit for their participation.

4.1.2 | Materials

Emotional stimuli were 32 audio recordings of actors (half male, half female) performing happy (“amused”) or angry vocal expressions using two pseudo-speech sentences, taken from the Geneva Multimodal Emotion Portrayals set (GEMEP; Bänziger, Mortillaro, & Scherer, 2012). We selected stimuli that were highly recognizable (all over 75%), based on the norms provided with the GEMEP set. All recordings had their maximal amplitude normalized to −1 dB. Silent parts were trimmed off, leaving a set that ranged in length from 1,235 to 3,747 ms ($M = 2{,}132.44$ ms, $SD = 631.11$).

4.1.3 | Procedure, design, and data analysis

Figure 5 presents the time course of a single trial. Each trial started with a fixation cross appearing for either 1,000, 1,200, or 1,400 ms. Then, an emotional stimulus was played to participants’ earphones simultaneously with the screen changing to either green or purple. As in the previous experiments, participants’ task was to either smile or frown, as quickly as possible, in response to the color. The exact matching between instruction and color was counterbalanced across participants. The trial ended with a 2,000 ms black screen. All other aspects of the procedure, as well the design and data analysis were the same as in experiments 1 and 2.

4.1.4 | Power

Power analysis was conducted using GLIMMPSE software (Kreidler et al., 2013), based on the data from experiment 2. In experiment 2, the total standard deviation was 106 ms, the correlation between compatible and incompatible trials was 0.94 and the correlation between muscles was 0.88. Together with the means reported for experiment 2, using these parameters in a repeated measures design indicated that a sample size of 24 should be sufficient to detect the effect with alpha level of 0.05 and power of 0.8.

4.2 | Results

On average, participants responded correctly and reliably on 74% of the trials ($SD = 15.59$). As before, only correct and reliable trials were used in the analysis. Three participants with exceptionally low percent of correct and reliable trials (<50%) were excluded entirely.

The internal consistency of the task, as indicated by a split-half reliability, was high (See Table S1 in the Supporting Information). Average RT are presented in Figure 6 and average time courses of the EMG response are presented in Figure S3 in the Supporting Information. The repeated measures ANOVA yielded a main effect of compatibility, $F(1,20) = 5.11$, $p = .035$, $\eta_p^2 = 0.203$, as well as an interaction between compatibility and task, $F(1,20) = 4.35$, $p = .050$, $\eta_p^2 = 0.179$. Post hoc comparisons

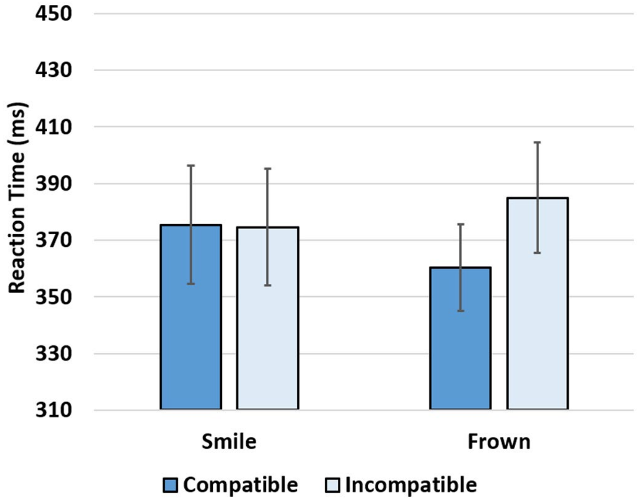

FIGURE 6 RT as a function of compatibility and task in experiment 3. RT in the frown task were faster in compatible, compared to incompatible trials. Error bars represent standard errors of the means

showed that frowning was faster in compatible, compared to incompatible trials, $t(20) = 2.90$, $p = .009$, but there was no difference in RT for smiling ($p > .05$). Incompatible trials had more miss errors than compatible trials and in smiling (but not frowning), incompatible trials also had more errors of responding with both muscles (see Supporting Information).

4.3 | Discussion

Experiment 3 investigated the facial SRC effect to emotional vocalizations. The perceived expressions—pseudo-sentences uttered in a happy or angry tone of voice—involved different motor actions than needed for smiling or frowning. Yet, we found faster frowning to angry, compared to happy vocalizations. While smiling did not show the same effect, our results do demonstrate that the facial SRC effect can be elicited by emotional expressions that do not match topographically.

The lack of effect in the smiling task is at odds with some previous mimicry findings showing both corrugator and zygomatic activity in response to emotional vocalizations (Hawk et al., 2012; Sestito et al., 2013). However, some differences between the paradigms should be considered. First, these studies used block designs, where stimuli of the same emotion were repeated throughout the block. This design could result with mood induction, which in turn, could facilitate the compatible facial expression. Such results were previously found in response to emotionally evocative sounds such as erotic moans, crowd cheer, or attack sounds (Verona, Patrick, Curtin, Bradley, & Lang, 2004). Indeed, smiling was correlated with self-reported happiness following the happy block (Study 2; Hawk et al., 2012). Second, both these studies used affect bursts, such as vocalizations of cries and laughter, while we used verbal vocalizations. Indeed, in a mimicry study that did use verbal vocalizations (emotional intonations of the name “Sara”), only the corrugator, but not the orbicularis oculi, showed a significantly different response for angry, compared to content expressions (Hietanen et al., 1998).

A few explanations could possibly account for this effect. First, hearing speech may create a tendency to activate the muscles around the mouth. An example to such mimicry was found in response to videos of people stutter (Berger & Hadley, 1975). This could obscure the difference between conditions in the zygomatic muscle, while not affecting the corrugator muscle. Interestingly, while RT for smiling in the incompatible condition were similar to experiment 1 and 2, the compatible condition was slower and similar to the incompatible condition. This could suggest that both angry and happy verbal expressions were somewhat incompatible with the smiling task.

Second, it should be noted that while the stimuli were more than a second long, it only took participants around 300 ms to respond. While speculative, if the angry stimuli were recognized by that time, but the happy stimuli were not, it could account for our results. The recognized angry stimuli would be congruent with frowning and incongruent with smiling, but the unrecognized happy stimuli would be incongruent with both tasks, creating an SRC effect for frowning, but not for smiling. This could also explain the opposite pattern of effect in the error analysis. Recognizing the angry stimuli would elicit more erroneous frown responses in the smile task, but the unrecognized happy stimuli would not create such an effect in the frown task.

To investigate this point further, we conducted an additional emotion recognition experiment (See the Supporting Information for a detailed description). One group of participants listened to the vocal stimuli used in experiment 3 and another group listened to a trimmed version of the same stimuli, leaving only the first 300 milliseconds. As predicted, we found that recognition was poorer for the trimmed, compared to the full-length stimuli, and for happy compared to angry stimuli. The disadvantage of happy stimuli was especially pronounced in the trimmed stimulus set. These findings suggest that quickly identifying the emotion in the happy stimuli was indeed harder. However, even in the short version, both happy and angry stimuli were recognized better than chance. This confirmed that even the first 300 milliseconds of the vocal expression convey enough information for the emotion to be recognized. Thus, while poor recognition of the happy stimuli could contribute to the effect, it probably cannot fully explain our pattern of results. Future studies using different muscles or different SOAs could further test these explanations.

5 | GENERAL DISCUSSION

Our aim in the present study was to challenge the matched motor hypothesis using a stimulus-response compatibility paradigm. Specifically, we looked at the case of producing emotional facial expressions while perceiving emotional vocalizations and body postures expressing the same or a different emotion. We predicted that this will result in a compatibility effect, even though the perceived and produced actions did not topographically match.

Experiment 1 was a conceptual replication of the known SRC effect of emotional expressions (Lee et al., 2008; Otte, Habel, et al., 2011; Wild et al., 2003). Participants responded to color cues by smiling and frowning, while watching task-irrelevant pictures of actors smiling and frowning. As expected, we found that participants were faster to respond while watching compatible facial expressions, compared to incompatible ones.

Experiment 2 directly tested the importance of topographic compatibility for this effect, by replacing the facial stimuli with emotional body postures. Even though now, perceived and produced actions involved completely different body parts, a similar compatibility effect emerged. This finding supports our hypothesis that topographic compatibility is not necessary for the SRC effect of emotional expressions.

Experiment 3 extended these findings to the auditory modality. The visual stimuli of emotional body postures were replaced with auditory stimuli of emotionally expressive utterances. As in experiment 2, the motor actions used for vocal expressions were different than the facial actions participants had to perform. Nevertheless, RT for frowning (though not for smiling) were faster when hearing a compatible, compared to an incompatible vocal expression. These results further demonstrate that perceiving a facial expression is not required to elicit facial SRC effects in response to emotional expressions.

All in all, our findings suggest that the tendency to match observed emotional expressions does not necessarily depend on the action's topography. In that, our findings are in line with mimicry studies that showed spontaneous facial activity in response to passive perception of emotional body (Magnée et al., 2007; Tamietto et al., 2009) and vocal (Hawk et al., 2012; Hietanen et al., 1998; Sestito et al., 2013) expressions. However, to the best of our knowledge, this is the first study to show this using SRC, a paradigm that was often thought to require topographic compatibility. Thus, our results demonstrate that the effect is not paradigm specific. These results provide converging evidence against the necessity of topographic compatibility and are at odds with the matched motor hypothesis.

Our study found there is a tendency to facially react to different types of emotional expressions, regardless of action topography. These results suggest that topographic compatibility is not necessary for the facial effect to emotional expressions. However, topographic compatibility could be contributing to the effect in the case of facial expressions. Indeed, the SRC effect found in response to facial expressions in experiment 1 was larger than the effects to body and vocal expressions in experiments 2 and 3, which could point at this direction. Future studies could further test the relative contribution of topographic versus non-topographic mechanisms by directly comparing different stimulus types within the same experiment.

If the tendency to match observed emotional expressions does not depend on topography, what does it depend on? Research suggests there might be multiple possible causes besides topography for matching a perceived expression. First, it has been suggested that emotion induced by the stimulus may have a role in the effect (Dimberg et al., 2002; Magnée et al., 2007; Moody, McIntosh, Mann, & Weisser, 2007; Tamietto et al., 2009). According to this view, perceiving emotional expressions elicits an emotional reaction, which activates an affect program (Dimberg et al., 2002; Magnée et al., 2007) or an action tendency (Moody et al., 2007) that facilitates the facial reaction. Indeed, observing emotional displays may evoke congruent emotional experiences in the observer (Hess & Blairy, 2001; Olszanowski, Wróbel, & Hess, 2020; Papousek, Schulter, & Lang, 2009; Wild, Erb, & Bartels, 2001). Other emotionally evocative stimuli, such as images of emotional scenes or words of positive and negative valence, were also shown to affect facial SRC responses (Chiew & Braver, 2010; Dimberg et al., 2002; Kozlik & Neumann, 2017; Neumann, Hess, Schulz, & Alpers, 2005). Moreover, fMRI studies found correlations between facial reactions to facial expressions and neural activations in the insula and amygdala, that are related to emotional processing (Lee et al., 2008; Rymarczyk et al., 2018).

Alternatively, action compatibility could play a role. It was found that opening or closing the mouth was affected by observing a hand opening or closing (Leighton & Heyes, 2010). It could be that in our case, expressing anger or happiness with the face is affected by observing expressions of anger and happiness with the body or hearing such vocal expressions. So, it is possible that here too the action compatibility is the crucial factor.

Stimulus-response associations are another mechanism that could explain our results. It has been suggested that the classic facial SRC effect is based on long-term associations between perceived and produced facial expressions (Kozlik & Neumann, 2017). A similar explanation was given by the Associative Sequence Learning theory (Brass & Heyes, 2005; Cook et al., 2014), regarding automatic imitation of hand movements and other motor actions. Interestingly, Heyes (2010) predicted that experience with correlated observation and execution of *dissimilar* actions could produce a tendency to respond with a different action than the one observed

(Heyes, 2010). In real-life, faces, bodies, and vocalizations are usually all experienced together. Therefore, life-long experience with emotional expressions may have created similar associations between perceived body postured or emotional vocalizations and produced facial expressions, which could account for the effect.

Finally, theories of embodied simulation should be considered (e.g., Niedenthal et al., 2010; Winkielman, Coulson, & Niedenthal, 2018; Wood et al., 2016). According to these views, while trying to infer another's emotional state, observers simulate the neural activity associated with the perceived expression. This subthreshold sensorimotor activation may then induce in the observer a related emotion state or an emotion concept. Thus, each of the sensorimotor activity, emotion state, or activated concept may facilitate the tendency to respond with a matching facial expression.

Taken together, valence, action compatibility, stimulus-response associations, and simulation processes may each create an effect. Our current analysis focused on topographic compatibility and showed that it is not necessary, though it could be contributing to the effect of facial expressions. Whether any of these other factors is necessary or whether their effect is additive warrants further investigation.

It is worth noting that, similar to most studies in the field, our stimuli consisted of posed stereotypical expressions, which may lack ecological validity (Abramson, Marom, Petranker, & Aviezer, 2017; Atias et al., 2019). Moreover, our visual stimuli were static rather than dynamic images. Dynamic stimuli better resemble real-life expressions and were shown to facilitate emotion recognition (Yitzhak, Gilaie-Dotan, & Aviezer, 2018). While the stimuli were ideal for maintaining high standardization in the experiment, their characteristics may influence the effect of topographic compatibility in a way that is somewhat different than real-life. Our auditory stimuli were, off course, dynamic, but were nonetheless acted. Future work could try to overcome this limitation by extending our findings to other stimuli or to more naturalistic settings.

Other directions for future research may include direct comparisons between facial SRC and mimicry. Both paradigms were used as measures of the tendency to match emotional expressions. However, clinical conditions affected mimicry and SRC differently (Chechko et al., 2016; Press et al., 2010; Schulte-Rüther et al., 2017). Moreover, direct comparisons between other related phenomena suggested differences in underlying mechanisms (Genschow et al., 2017; Ramsey, 2018). In order to keep using those paradigms in research it is crucial to establish their validity. Similarly, emotional facial SRC was often considered a type of automatic imitation (Chechko et al., 2016; Otte, Habel, et al., 2011; Press et al., 2010; Schulte-Rüther et al., 2017). In that case too, it would be highly beneficial to directly compare the two paradigms to either validate or refute this assumption.

Previous research has used the SRC effect of emotional facial expressions as a marker of automatic mimicry or mirror neuron system activation (Chechko et al., 2016; Press et al., 2010; Schulte-Rüther et al., 2017). Used with special populations, such as people with autistic spectrum conditions and schizophrenia, findings that were comparable to controls were taken as evidence for intact mimicry or an intact mirror neuron system. The abilities of "mimicry" or "mirroring" are usually thought of as involving one-to-one mapping of actions or basic matching of motor movements. However, our findings suggest that the abilities marked by the SRC effect may be broader. Whether it is matching of action meaning, matching of intention, or just a stimulus-response association, other perspectives need to be considered regarding the importance of such studies to the populations involved.

To conclude, our study investigated the automatic tendency to match observed emotional expressions using an SRC paradigm. Contrary to common arguments, our findings suggest that this automatic effect does not necessarily rely on topographic matching. Gaining better understanding of the mechanisms behind this effect is critical for interpreting past results, as well as for advancing future studies.

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DATA AVAILABILITY STATEMENT

All data, stimuli, and code will be made available from the authors upon request. The experiments were not preregistered.

AUTHOR CONTRIBUTION

Galit Shaham: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization, Writing-original draft; Marcello Mortillaro: Conceptualization, Methodology; Hillel Aviezer: Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Writing-review & editing.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Supplementary Material

Table S1. Split-half reliability by muscle and condition

Figure S1. Average time course of the EMG response as a function of compatibility and task in experiment 1. The middle bold line represents the average EMG response, surrounded by two dashed lines representing the standard deviation from the mean. Time is presented from onset of the color cue. EMG response in each trial was baseline corrected to the 500 ms. prior to the color cue and averaged separately for each muscle and condition across trials and participants. Zyg = Zygomatic muscle. Corr = Corrugator muscle.

Figure S2. Average time course of the EMG response as a function of compatibility and task in experiment 2. The middle bold line represents the average EMG response, surrounded by two dashed lines representing the standard deviation from the mean. Time is presented from onset of the color cue. EMG response in each trial was baseline corrected to the 500 ms. prior to the color cue and averaged separately for each muscle and condition across trials and participants. Zyg = Zygomatic muscle. Corr = Corrugator muscle.

Figure S3. Average time course of the EMG response as a function of compatibility and task in experiment 3. The middle bold line represents the average EMG response, surrounded by two dashed lines representing the standard deviation from the mean. Time is presented from onset of the color cue. EMG response in each trial was baseline corrected to the 500 ms. prior to the color cue and averaged separately for each muscle and condition across trials and participants. Zyg = Zygomatic muscle. Corr = Corrugator muscle.

Figure S5. Number of trials of each response type as a function of compatibility and task in experiment 1. There were fewer correct and reliable trials and more double and opposite errors in the incompatible, compared to the compatible condition. Error bars represent standard errors of the means.

Figure S6. Number of trials of each response type as a function of compatibility and task in experiment 2. There were fewer correct and reliable trials and more double errors in the incompatible, compared to the compatible condition. Error bars represent standard errors of the means.

Figure S7. Number of trials of each response type as a function of compatibility and task in experiment 3. There were more miss trials, and in the smiling task there were also fewer correct and reliable trials and more double errors, in the incomaptible, compared to the compatible condition. Error bars represent standard errors of the means.

Figure S8. Emotion recognition as a function of stimulus length and emotion in experiment S1. Emotion recognition was poorer for the trimmed (300 ms.), compared to the full-length stimuli, and for happy compared to angry stimuli. The disadvantage of happy stimuli was especially pronounced in the trimmed stimulus set. Error bars represent standard errors of the means.

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