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Research report

# Transcutaneous vagus nerve stimulation (tVNS) enhances recognition of emotions in faces but not bodies

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ABSTRACT

The polyvagal theory suggests that the vagus nerve is the key phylogenetic substrate enabling optimal social interactions, a crucial aspect of which is emotion recognition. A previous study showed that the vagus nerve plays a causal role in mediating people's ability to recognize emotions based on images of the eye region. The aim of this study is to verify whether the previously reported causal link between vagal activity and emotion recognition can be generalized to situations in which emotions must be inferred from images of whole faces and bodies. To this end, we employed transcutaneous vagus nerve stimulation (tVNS), a novel non-invasive brain stimulation technique that causes the vagus nerve to fire by the application of a mild electrical stimulation to the auricular branch of the vagus nerve, located in the anterior protuberance of the outer ear. In two separate sessions, participants received active or sham tVNS before and while performing two emotion recognition tasks, aimed at indexing their ability to recognize emotions from facial and bodily expressions. Active tVNS, compared to sham stimulation, enhanced emotion recognition for whole faces but not for bodies. Our results confirm and further extend recent observations supporting a causal relationship between vagus nerve activity and the ability to infer others' emotional state, but restrict this association to situations in which the emotional state is conveyed by the whole face and/or by salient facial cues, such as eyes.



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## 1. Introduction

Positive everyday social interactions contribute to promote physical and psychological health and well-being, and to allow adaptive behavior. It has been suggested that parasympathetic nervous system functioning mediates processes related to social behavior, and that its functioning can be indexed by activity of the vagus nerve (Hastings, Miller, Kahle, & Zahn-Waxler, 2014; Miller, Kahle, & Hastings, 2015; Porges, 2001; Stellar, Cohen, Oveis, & Keltner, 2015; but see; Grossman & Taylor, 2007). The vagus nerve is the tenth cranial nerve, also called the “wandering” nerve because of its broad distribution in the body: it extends from the head via the neck and thorax to the abdomen, and represents the greatest brain-body nexuses in the human nervous system (Yuan & Silberstein, 2016). The vagus nerve contributes to the coordination of the interplay between breathing and heart rate (Richter & Spyer, 1990; Thayer, Leorbroeks, & Stemberg, 2011), to control digestive processes (Stakenborg, Di Giovangiulio, Boeckxstaens, & Matteoli, 2013) and regulate inflammation response to disease (Pavlov & Tracey, 2012). Also, the vagus nerve helps humans nod their head and orienting their gaze towards other people, regulating facial expressions, listening and vocalizing (Porges, 2001; Stifter, Fox, & Porges, 1989; Thayer & Lane, 2000; Yang & Immordino-Yang, 2017).

According to the polyvagal theory (Porges, 2001, 2003, 2007; see also Darwin, 1872/1965), the vagus nerve can be regarded as the key phylogenetic element underpinning social engagement with the environment. The core aspect of this theory relies on the assumption that our physical body is elaborately designed to adapt and react rapidly to a variety of situations, without conscious awareness. Such a capacity is the result of a myelinated vagus nerve, which is found only in mammals. The polyvagal theory states that, during evolution, mammals have developed two vagal branches that evolved from different evolutionary responses. The dorsal vagal complex is the more primitive branch: it is dependent on the unmyelinated vagus, which regulates visceral functions and is responsible for initiating immobilization (freezing) behaviors. In contrast, the ventral vagal complex is the more evolved branch. This branch is dependent on the myelinated vagus, which exerts a control over the sympathetic nervous system by regulating the heart and the bronchi to foster calm and facilitate communication with the others. Moreover, the myelinated vagus nerve is associated with cranial nerves and, though this association, can regulate sociability by allowing people to synchronize their facial expression with others, make eye contact, modulate their voice and listen to others. The myelinated vagus nerve is therefore assumed to promote people's ability to understand and interpret social information, thereby enabling social exchange. Mounting correlational evidence has been compiled over the last years in support of the polyvagal theory and the link between vagal activity and social communication. Indeed, research has shown that vagal activity is positively associated with empathy, sympathy, with the ability to recognize emotions, and with prosocial behavior aimed at assisting others or alleviating others' suffering (Beauchaine, 2001; Butler, Wilhelm, & Gross, 2006; Eisenberg et al., 1997; Kogan et al., 2014; Kok & Fredrickson, 2010; Oveis et al., 2009; Porges, 2001; Quintana, Guastella, Outhred, Hickie, & Kemp, 2012; Wang, Lü, & Qin, 2013). More importantly for the purpose of the present study, a recent study by Colzato et al. (Colzato, Sellaro, & Beste, 2017) has provided the first direct evidence showing that the vagus nerve is causally involved in the recognition of social cues. In this study, a novel non-invasive brain stimulation technique, namely, transcutaneous (through the skin) vagus nerve stimulation (tVNS) was used to increase vagus nerve activation. This stimulation of the vagus nerve is achieved by applying a special earplug electrode to the outer ear to deliver electrical impulses to the auricular branch of the vagus nerve, that is, to the so-called Alderman's nerve or Arnold's nerve. By doing so, the afferent (i.e., the thick-myelinated Aβ) fibers of the Arnold's nerve are excited and the afferent signal propagates from peripheral nerves to the brainstem and, ultimately, to intracranial subcortical and cortical structures. Recent fMRI studies have shown that such a propagation produces a cerebral activation pattern (e.g., increased activation in the brainstem region including the locus coeruleus and nucleus of the solitary tract) that is similar to the one observed when stimulating the cervical branch of the vagus nerve (see Dietrich et al., 2008; Frangos, Ellrich, & Komisaruk, 2015; Kraus et al., 2007; Kreuzer et al., 2012). More importantly for the purpose of the present study, research has shown that tVNS is accompanied by a reduction in sympathetic activity and a shift in cardiac autonomic function toward parasympathetic/vagal predominance (Clancy et al., 2014).

Besides offering a non-invasive and effective way to stimulate the vagus nerve, tVNS has the additional advantage of allowing the implementation of a reliable sham (placebo) condition, which makes it a valuable research tool for assessing the possible causal contribution of the vagus nerve in mediating cognitive and social functioning in healthy humans (Beste et al., 2016; Colzato et al., 2017; Sellaro et al., 2015; Steenbergen et al., 2015; Van Leusden, Sellaro, & Colzato, 2015). Specifically, the sham condition is achieved by stimulating the earlobe to allow participants to experience the exact same mild and short-lasting skin sensations (i.e., tingling, itching and a moderate burning sensation under the stimulation electrode) without affecting the activity of the vagus nerve (Dietrich et al., 2008; Frangos et al., 2015; Kraus et al., 2007; Peuker & Filler, 2002). By using this technique, Colzato et al. (2017) were able to demonstrate that higher tVNS-induced vagus nerve activation significantly improved participants' performance on the Reading the Mind in the Eyes Test (RMET; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001a), which requires participants to infer what someone is feeling or thinking from images of the eye region. Given that the ability to recognize emotions plays a crucial role in enabling efficient social interactions (Adolphs, 1999; Frijda & Mesquita, 1994; Frith, 2009; Izard, 2007), the results reported by Colzato et al. (2017) can be taken as demonstration that the vagus nerve is in fact causally involved in facilitating social communication.

The aim of the current study is to verify whether the causal relationship between vagus nerve activation and emotion recognition reported by Colzato et al. (2017) can be generalized to situations in which people are required to infer emotions from images of whole faces and whole bodies. To verify this possibility, we asked participants to perform two emotion recognition tasks differing in the type of stimuli conveying the emotional expression (i.e., whole faces *vs.* whole bodies with a blurred face) while receiving, in two separate sessions, active and sham tVNS. To the extent to which the vagus nerve is causally involved in the recognition of others' emotions, the results reported by Colzato et al. (2017) should be replicated in situations in which emotions are conveyed by cues other than the eyes. Therefore, active, as compared to sham tVNS, is expected to improve participants' ability to recognize emotions, regardless of whether the emotion is conveyed by the whole face or by the whole body. Building on the Polyvagal theory, indeed, increased activation of the vagus nerve is expected to regulate sympathetic nervous system pathways to the heart, thereby promoting calm and relaxation, which are essential for allowing emotional experiences and social engagement (Porges, 2001, 2003, 2007).

However, some further considerations are necessary. Although there is evidence that the recognition of emotions is similar for facial and bodily expressions, important differences have also been reported (for reviews, see de Gelder, 2006, 2009). For instance, faces more than bodies offer a privileged and more automatic access to others' mental states, while bodies more than faces bias attention towards others' actions. This implies that when engaging in social interactions, people are more likely to rely on other people's facial expressions rather than on their body posture to assess whether the social environment is dangerous or not, which makes facial expressions the primary source of affective information humans can use to flexibly adapt to the external environment. Moreover, the vagus nerve is specifically connected to the muscles that control facial expressions and head movements, and is assumed to allow emotions people feel to be expressed in their faces and in the sound of their voices (Porges, 2007). Therefore, it is reasonable to expect tVNS to affect recognition of emotion from facial, but not from bodily expressions.

## 2. Materials and methods

### 2.1. Participants

A total of twenty-four healthy undergraduate students (15 females, 9 males, mean age = 20.71 years, SD = 2.35, range 18–28) at Leiden University took part in the experiment. Participants were recruited via the on-line SONA recruiting system, which asked for volunteers interested in participating in a two-sessions study on the effects of brain stimulation on decision-making. Volunteers who responded to the announcement were first screened individually by means of the Mini International Neuropsychiatric Interview (M.I.N.I.; Sheehan et al., 1998), which is a short, structured interview used in clinical research to assess the presence of a variety of psychiatric disorders and drug use (Colzato, van den Wildenberg, & Hommel, 2013b; Colzato, Szapora, Pannekoek, & Hommel, 2013a). Only volunteers who were reported to be healthy and to be free from drug use were selected and then further checked for exclusion criteria to tVNS protocol, such as, previous history of brain surgery, tumors, and neurological disorders, substance abuse or dependence, state of pregnancy, chronic or acute use of medications, susceptibility to seizures or migraine, presence of intracranial metal implantation, pacemaker and other implanted devices. Based on previously published studies (Beste et al., 2016; Colzato et al., 2017; Sellaro et al., 2015; Steenbergen et al., 2015), only those volunteers who fulfilled the inclusion criteria for tVNS protocol were allowed to participate in the study, provided that they met the additional inclusion criterion of being between 18 and 30 years of age.

All participants read and signed an informed consent during the first testing session. Participants were given an oral and written explanation of the study procedure and of the possible tVNS-induced adverse side-effects (i.e., itching and tingling skin sensation, skin-reddening, and headache), but all remained naïve about the experimental hypotheses and the different types of stimulation (active *vs.* sham). All the procedures conformed to the ethical standards of the 1975 Declaration of Helsinki, as revised in 1983, and the protocol was approved by the local ethical committee (Leiden University, Institute for Psychological Research). At the end of the second testing session, participants were debriefed about the nature of the study and the experimental hypothesis and received either course credits or 10 euros as a reimbursement for their participation.

### 2.2. Procedure

All participants took part in two counterbalanced experimental sessions, separated by one week, differing in the type of stimulation (active *vs.* sham) delivered before and during the execution of two emotion recognition tasks (i.e., facial and bodily emotion recognition tasks), and whose order was counterbalanced across participants. Following previous tVNS studies (Beste et al., 2016; Colzato et al., 2017; Sellaro et al., 2015; Steenbergen et al., 2015), in both sessions, participants performed the critical emotion recognition tasks twenty minutes after the stimulation was started to ensure sufficient activation of the vagus nerve at the time of their execution. All participants continued receiving tVNS while carrying out the emotion recognition tasks, which lasted for about 15 min.

To gather as much information as possible about our participants, at the beginning of each session, participants were required to fill in well-validated dispositional questionnaires aimed at assessing empathy baseline levels, autistic traits and alexithymia. Empathy baseline levels was measured by two questionnaires: the interpersonal reactivity index (IRI; Davis, 1983; Davis, 1980), and the Empathy Quotient (EQ; Baron-Cohen & Wheelwright, 2004). The presence of autistic-like traits was assessed by the Autistic Quotient (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001b). Lastly, the ability of participants in experiencing, expressing and describing their own emotional responses was assessed by means of the twenty-item Toronto Alexithymia scale (TAS-20; Bagby, Parker, & Taylor, 1994). While the IRI, the AQ and the TAS-20 were administered during the first testing session, the EQ was administered during the second session. A description of each questionnaire is provided in the following section.

At the end of each session, participants were interviewed about possible tVNS-induced adverse effects. To this end, they were asked to rate, on a 5-point (1–5) scale, how much they experienced the following sensations: headache, neck pain, nausea, muscle contraction in face and/or neck, stinging and/or burning sensation under the electrodes, uncomfortable (generic) feelings, and other sensations and/or adverse effects. None of the participants reported major complaints or discomfort during or after tVNS.

### 2.3. Questionnaires

*IRI.* The IRI provides a well-established tool for the multidimensional assessment of empathy. This self-report questionnaire is made of 28 items answered on a 5-point Likert scale (0 = does not describe me well; 4 = describes me very well). Items describe thoughts and feelings that can be experienced in a variety of situations. The questionnaire comprises four 7-item subscales, each assessing a separate facet of empathy. The perspective taking (PT) subscale assesses the general tendency to spontaneously assume the point of view of others; the fantasy scale (FS) assesses the tendency to imaginatively transpose oneself into fictional situations; the empathic concern (EC) scale assesses compassionate and sympathy feelings for others in need; the personal distress (PD) scale provides an indication of how much people are able to experience distress and discomfort when confronted with extreme distress in others. While fantasy and perspective taking subscales provides a measure of the cognitive component of empathy, empathic concern and personal distress subscales tap into its affective component (Davis, 1980; Davis, 1983).

*EQ.* The EQ is a well-established diagnostic tool to assess social impairments inherent in several disorders like autism and provides an accurate measure of trait empathy for the general population (Baron-Cohen & Wheelwright, 2004). This self-report questionnaire comprises 60 first-person statements (40 items related to empathy and 20 filler items), which the person has to rate as either “strongly agree”, “slightly agree”, “slightly disagree”, or “strongly disagree”. A single score, ranging from 0 (very low empathy) to 80 (very high empathy), is obtained, which provides an overall measure of empathy in terms of cognitive perspective taking, affective empathy, and social skills, without attempting to dissociate its cognitive and affective components.

*AQ.* The AQ is a clinical tool that measures the degree to which an adult in the general population has traits associated with the autistic spectrum (Baron-Cohen et al., 2001b). This questionnaire consists of 50 first-person statements concerning difficulties in the domains of communication, social skills, imagination, attention to detail and attention switching. For each statement, the individual has to rate how much s/he agrees by choosing between ‘definitely agree’, ‘slightly agree’, ‘slightly disagree’, or ‘definitely disagree’. Scores range from 0 to 50, with higher scores indicating autistic-like behavior.

*TAS-20.* The TAS-20 is one of the most commonly used instruments to measure alexithymia, which is referred to as a set of difficulties an individual may experience in identifying and describing one's own emotions and result in a tendency to minimize emotional experience and focus attention externally (Bagby et al., 1994). This questionnaire is made of 20 items that are rated using a 5-point Likert scale, where 1 = strongly disagree and 5 = strongly agree. The total alexithymia score is derived by summing up responses to all 20 items, with values ranging from 0 to 60. A total score equal to or less than 51 indicates no alexithymia, whereas a total score equal to or greater than 61 indicates alexithymia; scores between 52 and 60 indicates possible alexithymia. Items forming the TAS-20 can be further divided into three subscales exploring i) the difficulties in identifying emotions (7 items- Difficulty Identifying Feelings subscale); ii) the difficulties in describing emotions (5 items- Difficulty Describing Feelings subscale); and iii) the tendency to focus the attention externally (8 items- Externally-Oriented Thinking subscale).

### 2.4. Transcutaneous vagus nerve stimulation (tVNS)

To stimulate the vagus nerve, the NEMOS® tVNS device was used. This device has two parts: a stimulation unit, which generates electrical current, and a special ear electrode, which transfers electrical impulses from the stimulator to the surface of the skin via two titan electrodes mounted on a gel frame. Besides the two titan electrodes, the earlobe electrode is equipped with an earplug that is inserted in the auricle like an earphone, and that can be adjusted to properly fit the individual's ear (see Fig. 1 – panel A). In accordance with safety guidelines, the stimulation was always applied to the left ear to prevent the risk of incurring possible arrhythmic effects, which are rare and restricted to stimulation of the efferent vagal fibers connected to the right ear (Cristancho, Cristancho, Baltuch, Thase, & O'Reardon, 2011; Kreuzer et al., 2012; Nemeroff et al., 2006). After having carefully cleaned the ear electrode and the participant's left ear, the tVNS earplug was inserted in the auricle with the titan electrodes placed either in contact with the concha – for the active stimulation (see Fig. 1 – panel B) –, or in contact with the earlobe, i.e., a site free of cutaneous vagal innervation (Fallgatter et al., 2003; Peuker & Filler, 2002) – for the sham stimulation (see Fig. 1 – panel C).

For both active and sham stimulations, on and off periods of stimulation alternated every 30 s, with a stimulus intensity of 0.5 mA, and pulses delivered every 200–300 μs, at a frequency of 25 Hz, in keeping with the parameters adopted in previous studies (Beste et al., 2016; Colzato et al., 2017; Sellaro et al., 2015; Steenbergen et al., 2015).

### 2.5. Facial and bodily emotion recognition tasks

The ability to recognize emotions was assessed by means of two emotion recognition tasks differing for the type of stimuli conveying the to-be-recognized emotion, namely, facial or bodily expressions of emotion. The order of the two tasks was counterbalanced across participants. E-Prime 2.0 software system (Psychology Software Tools, Inc., Pittsburgh, PA) was used to generate the tasks and collect participants' responses.

Emotional face stimuli were selected from the Karolinska Directed Emotional Faces database (KDEF, Lundqvist, Flykt, & Öhman, 1998; Calvo & Lundqvist, 2008), whereas emotional body stimuli were selected from the Bodily Expression Action Stimulus Test (BEAST; de Gelder & Van den Stock, 2011). Given

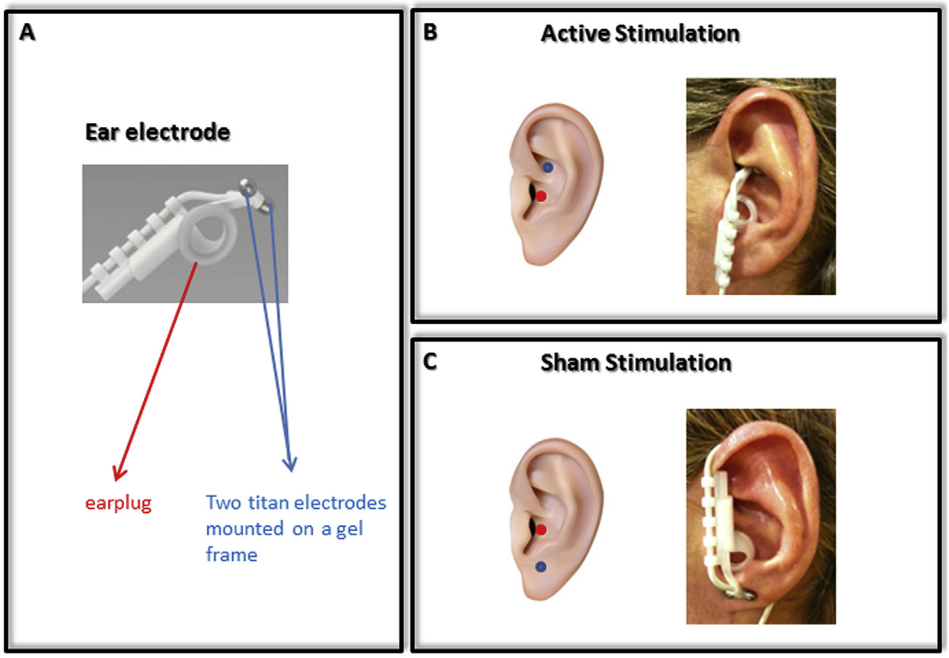


**Fig. 1 – A. Ear electrode that is used to deliver tVNS stimulation. The ear electrode consists of an earplug that is placed in the auricle like an earphone and two titan electrodes mounted on a gel frame that allow to generate and transfer electric impulses from the stimulator to the surface of the skin. B. Electrode position for the active stimulation. To deliver active stimulation, the two titan electrodes are placed on the outer auditory canal of the left ear. C. Electrode position for the sham stimulation. To deliver sham stimulation, the two titan electrodes are placed on the center of the left ear lobe.**

that participants were required to perform each task twice, namely, in two separate sessions, while receiving active tVNS and while receiving sham tVNS, for each task, two different lists of stimuli were selected to create two different task versions of equal difficulty. Participants were confronted with one version of the task during the first session and with the alternative version of the task during the second session. The order of the two task versions and the order of the two stimulation sessions (active and sham) were counterbalanced between participants, while, for each participant, the order between the face emotion recognition task and the body emotion recognition task was kept fixed across the two sessions.

Each version of the face emotion recognition task consisted of 80 pictures (20 for each emotion) of 20 female and 20 male emotional faces, whereas each version of the body emotion recognition task included 88 pictures (22 for each emotion) of 30 female and 14 male emotional bodies. A univariate analysis of variance (ANOVA) with the factors stimulus type (face *vs.* body) and task version (A *vs.* B) performed on the data published by the aforementioned studies (i.e., Calvo & Lundqvist, 2008; de Gelder & Van den Stock, 2011) showed that the facial and bodily emotion recognition tasks did not differ from each other in terms of overall difficulty, $F(1, 332) = 3.07$, $p = .08$, $\eta^2_p = .009$. Moreover, it confirmed that, for both tasks, the two versions were comparable in terms of difficulty, $Fs < 1$, $ps \geq .88$.

In both tasks, participants were presented with a central back-and-white target stimulus (i.e., a face without the body, or a body with a blurred face) and asked to choose which of four emotions (i.e., happy, fear, anger, and sad) better described what the person in the picture was feeling. The four emotional labels were displayed at the four corners of an imagined square surrounding the target picture, and participants had to click with the computer mouse on the chosen emotion. Each trial started with the presentation of the compound target picture–emotional labels, which remained on the screen until the participant responded. No response deadline was imposed. Trials were separated by a 500-ms blank screen. In each task, stimulus presentation was randomized.

### 2.6. *Statistical analyses*

For both emotion recognition tasks, the dependent variable was participants' accuracy in recognizing emotions. Following previous studies (e.g., Colzato et al., 2017; Domes, Heinrichs, Michel, Berger, & Herpertz, 2007; Guastella et al., 2010; Quintana et al., 2012), stimuli of each task were divided into two subsets of easy and difficult items. The two subsets were generated based on the median-split of item difficulty derived from the normative data provided by the two databases our stimuli were selected from, namely, the KDEF (Calvo & Lundqvist, 2008; Lundqvist et al., 1998) and the BEAST (de Gelder & Van den Stock, 2011), for emotional face and emotional body stimuli, respectively. Accuracy data from the two emotion recognition tasks were submitted to two separate repeated-measures ANOVAs with session (active *vs.* sham) and item difficulty (easy *vs.* difficult) as within-participant factors. A significant level of $p < .05$ was adopted for all statistical tests. In case of violation of sphericity

**Table 1 – Accuracy scores (±SEM) as a function of stimulation (active *vs*. sham) and item difficulty (easy *vs*. difficult items) for the facial and bodily emotion recognition tasks.**

| | Facial emotion recognition task | | Bodily emotion recognition task | |
|---|---|---|---|---|
| | Active | Sham | Active | Sham |
| Easy items | .97 (.01) | .97 (.01) | .96 (.01) | .96 (.01) |
| Difficult items | .88 (.01) | .82 (.01) | .83 (.02) | .83 (.02) |

assumption, Greenhouse–Geisser correction was applied and corrected *p* values were reported. Bonferroni post-hoc tests were performed to clarify mean differences in case of significant interactions. Data analyses were carried out using SPSS version 23 software (SPSS Inc., Chicago, IL, USA).

## 3. Results

### 3.1. Personality questionnaires

Overall, participants' scores on the questionnaires assessing trait empathy, autistic-like traits and alexithymia fell in the normal range: $IRI_{perspective\ taking}$ (17.96, SEM = .80), $IRI_{fantasy\ scale}$ (17.92, SEM = 1.03), $IRI_{empathic\ concern}$ (19.25, SEM = 1.04), $IRI_{personal\ distress}$ (14.08, SEM = .75), EQ (40.71, SEM = 2.41), AQ (17.71, SEM = 1.20), $TAS\text{-}20_{total\ score}$ (46.13, SEM = 1.37), $TAS\text{-}20_{difficulty\ identifying\ feelings}$ (15.33, SEM = .92), $TAS\text{-}20_{difficulty\ describing\ feelings}$ (12.83, SEM = .70), and $TAS\text{-}20_{externally\text{-}oriented\ thinking}$ (17.96, SEM = 1.09).

### 3.2. Facial emotion recognition task

ANOVA revealed three significant sources of variance. First, a significant main effect of item difficulty was found, $F(1,23) = 243.985$, $p < .001$, $\eta^2_p = .91$, which confirmed that accuracy was significantly lower for the difficult (.85, SEM = .011) than for the easy (.97, SEM = .005) items. More importantly, the main effect of session was significant too, $F(1,23) = 9.59$, $p = .005$, $\eta^2_p = .29$. As expected, participants showed higher accuracy in the active (.92, SEM = .009) as compared to the sham (.89, SEM = .008) session. The main effect of session interacted significantly with item difficulty, $F(1,23) = 32.858$, $p < .001$, $\eta^2_p = .59$. Bonferroni post-hoc tests showed that active tVNS improved participants' accuracy only for difficult items ($p < .001$, Cohen's $d = 1.0$), whereas comparable accuracy scores between active and sham sessions were observed for the easy items ($p = 1.0$, Cohen's $d = .14$). see Table 1 (fig. 2). Consistent with our expectations, tVNS was effective in improving people's ability to recognize emotions from the whole face.

### 3.3. Bodily emotion recognition task

ANOVA revealed only a significant source of variance, that is, the main effect of item difficulty, $F(1,23) = 91.553$, $p < .001$, $\eta^2_p = .80$, with participants showing higher accuracy in judging easy (.96, SEM = .006) than difficult (.83, SEM = .016) items. Neither the main effect of session, nor the interaction involving the two factors were significant, Fs < 1, ps ≥ .85, see Table 1 (fig. 2). Therefore, tVNS was not effective in modulating people's ability to recognize emotions from the whole body.

### 3.4. Additional analyses

#### 3.4.1. Bayesian analyses

The present results support the conclusion that the vagus nerve plays a causal role in the recognition of emotions from facial, but not from bodily expressions However, caution is needed to interpret these results, as null hypothesis significance testing (NHST) does not allow researchers to draw conclusions about non-significant effects – an issue that is even more relevant when the sample size is small. Therefore, we also analyzed our data within a Bayesian framework, which allows researchers to quantify and compare the relative likelihood of the data under two competing hypotheses, namely,

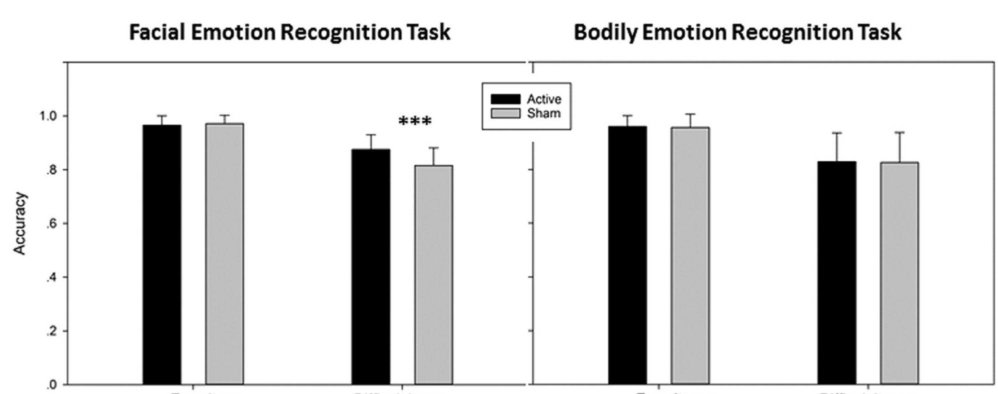


**Fig. 2 – Proportion of correct answers (i.e., accuracy scores) for the facial emotion recognition task (left-side panel) and the bodily emotion recognition task (right-side panel) as a function of stimulation (active *vs*. sham) and item difficulty (difficult *vs*. easy). Asterisks indicate significant differnces (****p* < .001). Vertical capped lines atop bars indicate standard deviation (SD).**

the alternative (H1) and the null (H0) hypothesis, as indexed by the Bayes factor (Morey & Rouder, 2015; Rouder, Morey, Speckman, & Province, 2012). Analyses were performed using JASP 0.8.2.0 software (available on https://jasp-stats.org/). The dataset and the results of the Bayesian analyses are archived in the Open Science Framework (OSF) and are available through https://osf.io/4xmec/?view_only=0485b997ad8f47cf8e79b7eed29a26c7.

A Bayesian repeated-measures ANOVA (using the default setting, namely, r scale fixed effect = .5; r scale random effects = 1; r scale covariates = .354; samples = Auto) was carried out to quantify evidence for the presence of a tVNS effect on emotion recognition ($BF_{10}$). A $BF_{10}$ larger than 1 indicates that the data are more likely to occur under H1 than under H0. For the facial emotion recognition task, results showed that, compared to the Null model, all but the session-only model received very strong support from the data ($BF_{Session}$ = .751, $BF_{Item\ difficulty}$ = 3.437e+20, $BF_{Session+Item\ difficulty}$ = 5.789e+21, $BF_{Session+Item\ difficulty+Session*Item\ difficulty}$ = 1.932e+24). Importantly, the model that received the most support against the Null model was the interaction model (Session + Item difficulty + Session*Item difficulty), which was preferred to model with the two main effects (Session + Item difficulty) by a Bayes factor of 334. Therefore, the observed data are 334 times more likely to have occurred under H1 than under H0, thereby providing overwhelming support (see Jeffreys, 1961; Lee & Wagenmakers, 2013) for the presence of a tVNS effect on facial emotion recognition when item difficulty is taken into consideration. For the bodily emotion recognition task, results showed that, compared to the Null model, all but the session-only model received very strong support from the data ($BF_{Session}$ = .212, $BF_{Item\ difficulty}$ = 2.334e+10, $BF_{Session+Item\ difficulty}$ = 4.884e+09, $BF_{Session+Item\ difficulty+Session*Item\ difficulty}$ = 1.421e+09). However, the model that received the most support against the Null model was the model that included item difficult only. Importantly, this model outperformed the two main effects model (Session + Item difficulty) by a Bayes factor of 4.78, and the interaction model (Session + Item difficulty + Session*Item difficulty) by a Bayes factor of 16.43 thereby providing moderate to strong evidence (see Jeffreys, 1961; Lee & Wagenmakers, 2013) for the lack of a significant effect of tVNS on bodily emotion recognition.

Taken together, the results of the Bayesian analyses are consistent with the conclusion that tVNS enhances recognition of emotions in faces, without affecting recognition of emotions in bodies.

### 3.4.2. *Gender-related differences*

Previous studies have suggested that females may tend to be more accurate than males in recognizing emotions (for a recent review, see Forni-Santos & Osório, 2015). To rule out the possibility that gender-related differences may have interacted with the observed effects, we re-ran the analyses with the inclusion of the additional factor of gender. For the facial emotion recognition, the ANOVA confirmed significant main effects of item difficulty, $F(1,23) = 218.45$, $p < .001$, $\eta^2_p = .91$, and session, $F(1,23) = 8.00$, $p = .01$, $\eta^2_p = .27$, and a significant interaction involving the two factors, $F(1,23) = 29.075$, $p < .001$, $\eta^2_p = .57$. Importantly, gender was not significant and did not interact with any factor, Fs < 1, ps ≥ .64. Likewise, for the bodily emotion recognition task, besides confirming the lack of any tVNS-induced effect on emotion recognition, Fs < 1, ps ≥ .63, the ANOVA failed to reveal any effect of gender or interactions between gender and any of the other factors, Fs ≤ 3.82, ps ≥ .06.

### 3.4.3. *Emotion-specific effects*

To assess whether tVNS affected recognition of specific emotions, regardless of the level of difficulty, we ran two ANOVAs with session (active *vs.* sham) and emotion (anger, fear, happy, sad) as within-participants factors. For the facial emotion recognition task, ANOVA revealed a significant main effect of session, $F(1,23) = 6.91$, $p = .015$, $\eta^2_p = .23$, with participants showing higher accuracy in the active (.93, SEM = .008) as compared to the sham (.91, SEM = .009) session. The main effect of emotion was significant too, F(3, 52.167) = 21.28, $p < .000$, $\eta^2_p = .48$. Consistent with the results reported by Calvo and Lundqvist (2008), Bonferroni post-hoc tests showed that participants were significantly better at recognizing happy faces (.997, SEM = .002) as compared to angry (.924, SEM = .019, $p < .001$), fearful (.870, SEM = .015, $p < .001$) or sad (.874, SEM = .011, $p < .001$) faces. Accuracy in recognizing fearful and sad faces was comparable ($p = 1$) and significantly lower than accuracy in recognizing angry faces ($p \leq .04$). Importantly, the interaction involving the factors session and emotion was not significant, F(3, 51.872) = 2.67, $p = .07$, $\eta^2_p = .10$, thereby suggesting that tVNS-induced improvement in emotion recognition was not restricted to any specific emotion. For the bodily recognition task, ANOVA revealed only a significant main effect of emotion, F(3, 38.033) = 21.84, $p < .001$, $\eta^2_p = .49$. Mirroring the results reported by de Gelder and Van den Stock (2011), Bonferroni post-hoc tests indicated that participants' accuracy was significantly lower in recognizing happy bodies (.787, SEM = .030) as compared to angry (.858, SEM = .017, $p < .001$), fearful (.941, SEM = .006, $p < .001$) or sad (.956, SEM = .009, $p < .001$) bodies. Moreover, accuracy in recognizing fearful and sad bodies was comparable ($p = 1$) and significantly higher than accuracy in recognizing angry bodies (ps < .005). Importantly, the main effect of session and the interaction between emotion and session were not significant, Fs < 1, ps ≥ .61.

## 4. Discussion

The present study sought to confirm and extend previous findings linking vagus nerve activity to social communication – the core assumption of the Polyvagal theory (Porges, 2001, 2003, 2007, 2011). In particular, building on recent results showing that vagus nerve activity causally contributes to the ability to recognize others' emotions based on photographs of the eye region (Colzato et al., 2017), we used tVNS with the goal to assess whether such a role is restricted to situations in which emotions are conveyed by the eyes or can generalize to situations in which emotions are conveyed by other cues, such as the whole face and/or the whole body. Results are straightforward in showing that vagus nerve activity plays a causal role in the recognition of emotions from facial, but not from bodily expressions. Indeed, we observed that active, as compared to sham tVNS, improved the ability to recognize emotions only when participants were required to infer others' emotional states from photographs of the whole faces, but not when they were required to infer the same emotional states from photographs of whole bodies without faces. Therefore, the present results suggest that facial expressions, compared to bodily expressions, are probably more powerful in informing about the nature of the situation people are engaged in, and are probably the primary source of information people can rely on to implement proper behaviors to meet the environmental demands. Such a dissociation may be accounted for by considering that the vagus nerve exerts a direct influence on the cranial nerves controlling facial expressions and allows establishment of eye contact (Porges, 2007).

Given that inferring others' emotional state is a vital social skill enabling people to understand and predict others' behavior during social interactions (Frijda & Mesquita, 1994; Frith, 2009; Izard, 2007), our results provide additional direct evidence corroborating previous correlational findings suggesting that the vagus nerve may be causally involved in processes related to social functioning (Hastings et al., 2014; Quintana et al., 2012; Stellar et al., 2015) as proposed by the Polyvagal theory (Porges, 2001, 2003, 2007, 2011). As previously mentioned, according to the Polyvagal theory, activity of the vagus nerve can be taken to reflect people's ability to recognize and respond to social cues, which is fundamental to implement physiological adaptation to encourage or discourage social engagement with the environment (Porges, 2001, 2003, 2007, 2011). Our findings, along with the results reported by Colzato et al. (2017), confirm that the vagus nerve plays a causal role at least in the recognition of emotional expressions, although such a role is restricted to recognition of emotional facial expressions or salient facial cues, like the eyes. This is not to deny, however, that more research is needed to confirm such a role, as evidence exists that challenges some of the assumptions the Polyvagal theory is grounded on (see Grossman & Taylor, 2007).

Moreover, some limitations and considerations concerning these results need to be discussed here. First of all, we did not directly measure participants' baseline vagal activity, which can be indexed by resting-state heart rate variability (Berntson et al., 1997; Quintana et al., 2012) and/or by respiratory sinus arrhythmia (Berntson, Sarter, & Cacioppo, 1998; Kogan et al., 2014). In a previous study, a quadratic relationship between vagal activity and prosocial behavior has been reported, with both very high and very low levels of vagal activity being detrimental to social functioning (Kogan et al., 2014). Therefore, it would be crucial for follow up studies to assess whether individual differences in baseline vagal activity can mediate tVNS effectiveness in improving emotion recognition. Ideally, one would expect only participants with low vagal activity to benefit from active tVNS. Moreover, we did not verify tVNS effectiveness in increasing vagal activity. Therefore, it would be optimal for future studies to include such an assessment, for instance, by measuring vagus-evoked potentials (Fallgatter et al., 2003) and by assessing tVNS-induced changes in heart rate variability. Second, we did not assess explicitly participants' blinding by asking them if they could guess the stimulation received. However, even though it would be advisable for further studies to include such an assessment, participants' expectations concerning the stimulation received are unlikely to account for the fact that tVNS-induced changes in emotion recognition were restricted to faces, but not to bodily stimuli. Third, increasing evidence suggests that emotional facial expression recognition can be influenced by concomitant information concerning the body expression (Kret & de Gelder, 2013; Kret, Roelofs, Stekelenburg, & de Gelder, 2013; Meeren, van Heijnsbergen, & de Gelder, 2005; Van den Stock, Righart, & de Gelder, 2007), and the ambient context (Kret & de Gelder, 2012; Righart & de Gelder, 2006, 2008). For instance, it has been found that when presenting participants with face-body compound stimuli, participants rely more on bodies when conflicting information is presented (Meeren et al., 2005; Van den Stock et al., 2007). Therefore, it would be of interest for future studies to use face-body (congruent and incongruent) compound stimuli to assess whether and to what extent tVNS can modulate the recognition of emotional faces accompanied by whole body expressions. Fourth, research has suggested that the preferential processing of either faces or bodies varies as a function of the distance from the stimulus. Specifically, while whole faces, and especially the eye regions, are preferentially processed in situations in which the emotional stimulus is close enough to the perceiver, whole body expressions are preferentially processed in situations in which the stimulus is far away from the perceiver (Johnson, 2005). Therefore, it would be valuable for further studies to use techniques, like virtual reality, to manipulate the distance between the emotional stimulus and the perceiver, and assess whether the chance of observing tVNS-induced changes in facial and bodily emotion recognition can vary as a function of it. Fifth, there is evidence that perception of emotion in the voice can play a powerful communicative function (Pourtois, de Gelder, Bol, & Crommelinck, 2005). Given that the vagus nerve is also assumed to be involved in regulating sociability by helping people to modulate their voice and listen to others, it would be interesting to verify whether the reported findings documenting improved tVNS-induced emotion recognition can also extend to the recognition of emotions in voices. Finally, it would be also relevant to assess whether the vagus nerve plays a causal role in modulating other social abilities.

To conclude, our findings provide direct support for the Polyvagal theory (Porges, 2001, 2003, 2007, 2011). Moreover, the reported results add to the emerging literature suggesting that tVNS is an effective tool to measure cognitive and social functioning (Beste et al., 2016; Colzato et al., 2017; Sellaro et al., 2015; Steenbergen et al., 2015), and provide support for the recent proposal that it can be a promising tool for the treatment of pathologies associated with dysfunction in the vagus nerve and impaired social functioning, such as the Autism Spectrum Disorder (see Jin & Kong, 2016).

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## REFERENCES


Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Sciences, 3*(12), 469–479.

Bagby, R. M., Parker, J. D., & Taylor, G. J. (1994). The twenty-item Toronto Alexithymia Scale—I. Item selection and cross-validation of the factor structure. *Journal of Psychosomatic Research, 38*(1), 23–32.

Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: An investigation of adults with asperger syndrome or high functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders, 34*(2), 163–175.

Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001a). The "reading the mind in the eyes" test revised version: A study with normal adults, and adults with asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry, and Allied Disciplines, 42*(2), 241–251.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001b). The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders, 31*(1), 5–17.

Beauchaine, T. (2001). Vagal tone, development, and Gray's motivational theory: Toward an integrated model of autonomic nervous system functioning in psychopathology. *Development and Psychopathology, 13*(2), 183–214.

Berntson, G. G., Bigger, J. T., Eckberg, D. L., Grossman, P., Kaufmann, P. G., Malik, M., et al. (1997). Heart rate variability: Origins, methods, and interpretive caveats. *Psychophysiology, 34*(6), 623–648.

Berntson, G. G., Sarter, M., & Cacioppo, J. T. (1998). Anxiety and cardiovascular reactivity: The basal forebrain cholinergic link. *Behavioural Brain Research, 94*(2), 225–248.

Beste, C., Steenbergen, L., Sellaro, R., Grigoriadou, S., Zhang, R., Chmielewski, W., et al. (2016). Effects of concomitant stimulation of the GABAergic and norepinephrine system on inhibitory control - a study using transcutaneous vagus nerve stimulation. *Brain Stimulation, 9*(6), 811–818. https://doi.org/10.1016/j.brs.2016.07.004.

Butler, E. A., Wilhelm, F. H., & Gross, J. J. (2006). Respiratory sinus arrhythmia, emotion, and emotion regulation during social interaction. *Psychophysiology, 43*(6), 612–622. https://doi.org/10.1111/j.1469-8986.2006.00467.x.

Calvo, M. G., & Lundqvist, D. (2008). Facial expressions of emotion (KDEF): Identification under different display-duration conditions. *Behavior Research Methods, 40*(1), 109–115.

Clancy, J. A., Mary, D. A., Witte, K. K., Greenwood, J. P., Deuchars, S. A., & Deuchars, J. (2014). Non-invasive Vagus nerve stimulation in healthy humans reduces sympathetic nerve activity. *Brain Stimulation, 7*(6), 871–877. https://doi.org/10.1016/j.brs.2014.07.031.

Colzato, L. S., Sellaro, R., & Beste, C. (2017). Darwin revisited: The vagus nerve is a causal element in controlling recognition of other's emotions. *Cortex; a Journal Devoted To the Study of the Nervous System and Behavior, 92*, 95–102. https://doi.org/10.1016/j.cortex.2017.03.017.

Colzato, L. S., Szapora, A., Pannekoek, J. N., & Hommel, B. (2013a). The impact of physical exercise on convergent and divergent thinking. *Frontiers in Human Neuroscience, 7*, 824. https://doi.org/10.3389/fnhum.2013.00824.

Colzato, L. S., van den Wildenberg, W. P., & Hommel, B. (2013b). The genetic impact (C957T-DRD2) on inhibitory control is magnified by aging. *Neuropsychologia, 51*(7), 1377–1381.

Cristancho, P., Cristancho, M. A., Baltuch, G. H., Thase, M. E., & O'Reardon, J. P. (2011). Effectiveness and safety of vagus nerve stimulation for severe treatment-resistant major depression in clinical practice after FDA approval: Outcomes at 1 year. *The Journal of Clinical Psychiatry, 72*(10), 1376–1382. https://doi.org/10.4088/JCP.09m05888blu.

Darwin, C. (1872/1965). *The expression of emotions in man and animals* (Vol. 526). University of Chicago press.

Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology, 44*(1), 113–126. https://doi.org/10.1037/0022-3514.44.1.113.

Davis, M. H., & Association, A. P. (1980). *A multidimensional approach to individual differences in empathy*. American Psychological Association. Retrieved from https://books.google.nl/books?id=HUQHcgAACAAJ.

Dietrich, S., Smith, J., Scherzinger, C., Hofmann-Preiß, K., Freitag, T., Eisenkolb, A., et al. (2008). A novel transcutaneous vagus nerve stimulation leads to brainstem and cerebral activations measured by functional MRI/Funktionelle Magnetresonanztomographie zeigt Aktivierungen des Hirnstamms und weiterer zerebraler Strukturen unter transkutaner Vagusnervstimulation. *Biomedizinische Technik/Biomedical Engineering, 53*(3), 104–111. https://doi.org/10.1515/BMT.2008.022.

Domes, G., Heinrichs, M., Michel, A., Berger, C., & Herpertz, S. C. (2007). Oxytocin improves "mind-reading" in humans. *Biological Psychiatry, 61*(6), 731–733. https://doi.org/10.1016/j.biopsych.2006.07.015.

Eisenberg, N., Fabes, R. A., Shepard, S. A., Murphy, B. C., Guthrie, I. K., Jones, S., et al. (1997). Contemporaneous and longitudinal prediction of children's social functioning from regulation and emotionality. *Child Development, 68*(4), 642–664.

Fallgatter, A. J., Neuhauser, B., Herrmann, M. J., Ehlis, A.-C., Wagener, A., Scheuerpflug, P., et al. (2003). Far field potentials from the brain stem after transcutaneous vagus nerve stimulation. *Journal of Neural Transmission (Vienna, Austria: 1996), 110*(12), 1437–1443. https://doi.org/10.1007/s00702-003-0087-6.

Forni-Santos, L., & Osório, F. L. (2015). Influence of gender in the recognition of basic facial expressions: A critical literature review. *World Journal of Psychiatry, 5*(3), 342–351.

Frangos, E., Ellrich, J., & Komisaruk, B. R. (2015). Non-invasive access to the vagus nerve central projections via electrical stimulation of the external ear: fMRI evidence in humans. *Brain Stimulation, 8*(3), 624–636. https://doi.org/10.1016/j.brs.2014.11.018.

Frijda, N. H., & Mesquita, B. (1994). The social roles and functions of emotions. In S. Kitayama, & H. R. Markus (Eds.), *Emotion and culture: Empirical studies of mutual influence* (pp. 51–87). Washington: American Psychological Association. https://doi.org/10.1037/10152-002.

Frith, C. (2009). Role of facial expressions in social interactions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364*(1535), 3453–3458. https://doi.org/10.1098/rstb.2009.0142.

de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews Neuroscience, 7*(3), 242–249. https://doi.org/10.1038/nrn1872.

de Gelder, B. (2009). Why bodies? Twelve reasons for including bodily expressions in affective neuroscience. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364*(1535), 3475–3484. https://doi.org/10.1098/rstb.2009.0190.

de Gelder, B., & Van den Stock, J. (2011). The bodily expressive action stimulus test (BEAST). Construction and validation of a stimulus basis for measuring perception of whole body expression of emotions. *Frontiers in Psychology, 2*(181). https://doi.org/10.3389/fpsyg.2011.00181.

Grossman, P., & Taylor, E. W. (2007). Toward understanding respiratory sinus arrhythmia: Relations to cardiac vagal tone,

evolution and biobehavioral functions. *Biological Psychology, 74*(2), 263–285.
Guastella, A. J., Einfeld, S. L., Gray, K. M., Rinehart, N. J., Tonge, B. J., Lambert, T. J., et al. (2010). Intranasal oxytocin improves emotion recognition for youth with autism spectrum disorders. *Biological Psychiatry, 67*(7), 692–694. https://doi.org/10.1016/j.biopsych.2009.09.020.
Hastings, P. D., Miller, J. G., Kahle, S., & Zahn-Waxler, C. (2014). The neurobiological bases of empathic concern for others. In *Handbook of moral development*. Routledge. https://doi.org/10.4324/9780203581957.ch19.
Izard, C. E. (2007). Emotion Feelings Stem from Evolution and Neurobiological Development, Not From Conceptual Acts: Corrections for Barrett et al. (2007). *Perspectives on Psychological Science: A Journal of the Association for Psychological Science, 2*(4), 404–405. https://doi.org/10.1111/j.1745-6916.2007.00053.x.
Jeffreys, H. (1961). *Theory of probability* (3rd ed.). Oxford, UK: Oxford University Press.
Jin, Y., & Kong, J. (2016). Transcutaneous vagus nerve stimulation: A promising method for treatment of autism spectrum disorders. *Frontiers in Neuroscience, 10*(609). https://doi.org/10.3389/fnins.2016.00609.
Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience, 6*, 766–774.
Kogan, A., Oveis, C., Carr, E. W., Gruber, J., Mauss, I. B., Shallcross, A., et al. (2014). Vagal activity is quadratically related to prosocial traits, prosocial emotions, and observer perceptions of prosociality. *Journal of Personality and Social Psychology, 107*(6), 1051–1063. https://doi.org/10.1037/a0037509.
Kok, B. E., & Fredrickson, B. L. (2010). Upward spirals of the heart: Autonomic flexibility, as indexed by vagal tone, reciprocally and prospectively predicts positive emotions and social connectedness. *Biological Psychology, 85*(3), 432–436.
Kraus, T., Hösl, K., Kiess, O., Schanze, A., Kornhuber, J., & Forster, C. (2007). BOLD fMRI deactivation of limbic and temporal brain structures and mood enhancing effect by transcutaneous vagus nerve stimulation. *Journal of Neural Transmission (Vienna, Austria: 1996), 114*(11), 1485–1493. https://doi.org/10.1007/s00702-007-0755-z.
Kret, M. E., & de Gelder, B. (2012). Islamic headdress influences how emotion is recognized from the eyes. *Frontiers in Psychology, 3*(110). https://doi.org/10.3389/fpsyg.2012.00110.
Kret, M. E., & de Gelder, B. (2013). When a smile becomes a fist: The perception of facial and bodily expressions of emotion in violent offenders. *Experimental Brain Research, 228*(4), 399–410. https://doi.org/10.1007/s00221-013-3557-6.
Kret, M. E., Roelofs, K., Stekelenburg, J. J., & de Gelder, B. (2013). Emotional signals from faces, bodies and scenes influence observers' face expressions, fixations and pupil-size. *Frontiers in Human Neuroscience, 7*(810). https://doi.org/10.3389/fnhum.2013.00810.
Kreuzer, P. M., Landgrebe, M., Husser, O., Resch, M., Schecklmann, M., Geisreiter, F., et al. (2012). Transcutaneous vagus nerve stimulation: Retrospective assessment of cardiac safety in a pilot study. *Frontiers in Psychiatry, 3*(70). https://doi.org/10.3389/fpsyt.2012.00070.
Lee, M. D., & Wagenmakers, E. J. (2013). *Bayesian cognitive modeling: A practical course*. Cambridge University Press.
Lundqvist, D., Flykt, A., & Öhman, A. (1998). *The Karolinska directed emotional faces (KDEF). CD ROM from department of clinical neuroscience, psychology section, Karolinska institutet*.
Meeren, H. K. M., van Heijnsbergen, C. C. R. J., & de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences of the United States of America, 102*(45), 16518–16523. https://doi.org/10.1073/pnas.0507650102.
Miller, J. G., Kahle, S., & Hastings, P. D. (2015). Roots and benefits of costly Giving: Children who are more altruistic have greater autonomic flexibility and less family wealth. *Psychological Science, 26*(7), 1038–1045. https://doi.org/10.1177/0956797615578476.
Morey, R. D., & Rouder, J. N. (2015). *BayesFactor (Version 0.9.11-3) [Computer software]*.
Nemeroff, C. B., Mayberg, H. S., Krahl, S. E., McNamara, J., Frazer, A., Henry, T. R., et al. (2006). VNS therapy in treatment-resistant depression: Clinical evidence and putative neurobiological mechanisms. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology, 31*(7), 1345–1355. https://doi.org/10.1038/sj.npp.1301082.
Oveis, C., Cohen, A. B., Gruber, J., Shiota, M. N., Haidt, J., & Keltner, D. (2009). Resting respiratory sinus arrhythmia is associated with tonic positive emotionality. *Emotion (Washington, D.C.), 9*(2), 265–270. https://doi.org/10.1037/a0015383.
Pavlov, V. A., & Tracey, K. J. (2012). The vagus nerve and the inflammatory reflex—linking immunity and metabolism. *Nature Reviews Endocrinology, 8*(12), 743–754.
Peuker, E. T., & Filler, T. J. (2002). The nerve supply of the human auricle. *Clinical Anatomy (New York, N.Y.), 15*(1), 35–37. https://doi.org/10.1002/ca.1089.
Porges, S. W. (2001). The polyvagal theory: Phylogenetic substrates of a social nervous system. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology, 42*(2), 123–146.
Porges, S. W. (2003). Social engagement and attachment: A phylogenetic perspective. *Annals of the New York Academy of Sciences, 1008*, 31–47.
Porges, S. W. (2007). The polyvagal perspective. *Biological Psychology, 74*(2), 116–143. https://doi.org/10.1016/j.biopsycho.2006.06.009.
Porges, S. W. (2011). *The polyvagal theory: Neurophysiological foundations of emotions, attachment, communication, and self-regulation*. New York: W.W. Norton.
Pourtois, G., de Gelder, B., Bol, A., & Crommelinck, M. (2005). Perception of facial expressions and voices and of their combination in the human brain. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior, 41*(1), 49–59.
Quintana, D. S., Guastella, A. J., Outhred, T., Hickie, I. B., & Kemp, A. H. (2012). Heart rate variability is associated with emotion recognition: Direct evidence for a relationship between the autonomic nervous system and social cognition. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology, 86*(2), 168–172. https://doi.org/10.1016/j.ijpsycho.2012.08.012.
Richter, D. W., & Spyer, K. M. (1990). Cardiorespiratory control. In A. D. Loewry, & K. M. Spyer (Eds.), *Central regulation of autonomic function* (pp. 189–207). New York: Oxford University Press.
Righart, R., & de Gelder, B. (2006). Context influences early perceptual analysis of faces—an electrophysiological study. *Cerebral Cortex (New York, N.Y.: 1991), 16*(9), 1249–1257. https://doi.org/10.1093/cercor/bhj066.
Righart, R., & de Gelder, B. (2008). Rapid influence of emotional scenes on encoding of facial expressions: An ERP study. *Social Cognitive and Affective Neuroscience, 3*(3), 270–278. https://doi.org/10.1093/scan/nsn021.
Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology, 56*, 356–374.
Sellaro, R., van Leusden, J. W. R., Tona, K.-D., Verkuil, B., Nieuwenhuis, S., & Colzato, L. S. (2015). Transcutaneous vagus nerve stimulation enhances post-error slowing. *Journal of Cognitive Neuroscience, 27*(11), 2126–2132. https://doi.org/10.1162/jocn_a_00851.
Sheehan, D. V., Lecrubier, Y., Sheehan, K. H., Amorim, P., Janavs, J., Weiller, E., et al. (1998). The mini-international neuropsychiatric interview (M.I.N.I.): The development and validation of a structured diagnostic psychiatric interview for

DSM-IV and ICD-10. *The Journal of Clinical Psychiatry, 59*(Suppl. 20), 22–33;quiz 34–57.

Stakenborg, N., Di Giovangiulio, M., Boeckxstaens, G. E., & Matteoli, G. (2013). The versatile role of the vagus nerve in the gastrointestinal tract. *European Medical Journal Gastroenterology, 1*, 106–114.

Steenbergen, L., Sellaro, R., Stock, A.-K., Verkuil, B., Beste, C., & Colzato, L. S. (2015). Transcutaneous vagus nerve stimulation (tVNS) enhances response selection during action cascading processes. *European Neuropsychopharmacology: the Journal of the European College of Neuropsychopharmacology, 25*(6), 773–778. https://doi.org/10.1016/j.euroneuro.2015.03.015.

Stellar, J. E., Cohen, A., Oveis, C., & Keltner, D. (2015). Affective and physiological responses to the suffering of others: Compassion and vagal activity. *Journal of Personality and Social Psychology, 108*(4), 572–585. https://doi.org/10.1037/pspi0000010.

Stifter, C. A., Fox, N. A., & Porges, S. W. (1989). Facial expressivity and vagal tone in 5-and 10-month-old infants. *Infant Behavior and Development, 12*(2), 127–137.

Thayer, J. F., & Lane, R. D. (2000). A model of neurovisceral integration in emotion regulation and dysregulation. *Journal of Affective Disorders, 61*(3), 201–216.

Thayer, J. F., Loerbroks, A., & Sternberg, E. M. (2011). Inflammation and cardiorespiratory control: The role of the vagus nerve. *Respiratory Physiology & Neurobiology, 178*(3), 387–394.

Van Leusden, J. W. R., Sellaro, R., & Colzato, L. S. (2015). Transcutaneous vagal nerve stimulation (tVNS): A new neuromodulation tool in healthy humans? *Frontiers in Psychology, 6*(102). https://doi.org/10.3389/fpsyg.2015.00102.

Van den Stock, J., Righart, R., & de Gelder, B. (2007). Body expressions influence recognition of emotions in the face and voice. *Emotion (Washington, D.C.), 7*(3), 487–494. https://doi.org/10.1037/1528-3542.7.3.487.

Wang, Z., Lü, W., & Qin, R. (2013). Respiratory sinus arrhythmia is associated with trait positive affect and positive emotional expressivity. *Biological Psychology, 93*(1), 190–196. https://doi.org/10.1016/j.biopsycho.2012.12.006.

Yang, X. F., & Immordino-Yang, M. H. (2017). Culture and cardiac vagal tone independently influence emotional expressiveness. *Culture and Brain, 5*(1), 36–49.

Yuan, H., & Silberstein, S. D. (2016). Vagus nerve and vagus nerve stimulation, a comprehensive review: Part I: Headache. *Headache: The Journal of Head and Face Pain, 56*(1), 71–78. https://doi.org/10.1111/head.12647.