The Power of a Handshake: Neural Correlates of Evaluative Judgments in Observed Social Interactions

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Abstract

■ Effective social interactions require the ability to evaluate other people's actions and intentions, sometimes only on the basis of such subtle factors as body language, and these evaluative judgments may lead to powerful impressions. However, little is known about the impact of affective body language on evaluative responses in social settings and the associated neural correlates. This study investigated the neural correlates of observing social interactions in a business setting, in which whole-body dynamic stimuli displayed approach and avoidance behaviors that were preceded or not by a handshake and were followed by participants' ratings of these behaviors. First, approach was associated with more positive evaluations than avoidance behaviors, and a handshake preceding social interaction enhanced the positive impact of approach and diminished the negative impact of avoidance behavior on the evaluation of social interaction. Second, increased sensitivity to approach than to avoidance behavior in the amygdala and STS was linked to a positive evaluation of approach behavior and a positive impact of handshake. Third, linked to the positive effect of handshake on social evaluation, nucleus accumbens showed greater activity for Handshake than for No-handshake conditions. These findings shed light on the neural correlates of observing and evaluating nonverbal social interactions and on the role of handshake as a way of formal greeting. ■

INTRODUCTION

Effective social interaction requires the ability to evaluate other people's actions and intentions, which may lead to powerful impressions. When interacting with unknown others for whom no relevant information is available, people rely on a variety of factors, such as physical appearance, verbal behavior (Ames, Fiske, & Todorov, 2011), as well as subtle nonverbal behavior, or affective body language (de Gelder et al., 2010), as cues to form an impression. In the Hollywood movie *Hitch* (2005), portrayed by Will Smith, Hitch provides dating advice to a client saying that "60% of all human communication is nonverbal, body language; 30% is your tone, so that means 90% of what you're saying ain't coming out of your mouth."

The importance of nonverbal behavior in drawing inferences about others is supported by scientific evidence showing that nonverbal behavior has five times the impact of verbal messages on judgments of a communicator's friendliness and liking for the message recipient (Argyle, 1988). Subtle cues conveyed through body language or physical touch, such as a handshake or a gentle touch on the shoulder, can lead to positive effects on behavior, reflected in increased feelings of security when making risky financial decisions (Levav & Argo, 2010) or better evaluations and better tips (Stephen & Zweigenhaft, 1986). Despite its crucial role in guiding everyday social interactions, little is known about the impact of affective body language on behavioral evaluations in social settings and the associated neural correlates. Here, we investigated the neural correlates of observing approach- and avoidance-inducing body signals in dynamic social interactions, using fMRI.

During social interactions, people engage in active social perception processes, such as attending to others' face and body language, to evaluate the social situation. The vast majority of studies investigating the neural correlates of social cognition tended to focus on faces or static whole-body stimuli (van de Riet, Grezes, & de Gelder, 2009; Meeren, Van Heijnsbergen, & de Gelder, 2005). These studies indicate that the neural network underlying whole-body perception partly overlaps with the face network (de Gelder et al., 2010; Peelen & Downing, 2007; de Gelder & Hadjikhani, 2006) and involves the amygdala (AMY), the fusiform gyrus, and the STS. However, although both faces and bodies are salient and familiar in everyday life, conveying information about the internal states that is essential for social interactions, only bodily expressions allow perception of the action and of its emotional significance (Sinke, Kret, & de Gelder, 2012), hence prepare the perceiver for adaptive actions.

Although more limited in number compared with studies using static stimuli, recent studies using dynamic bodily

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expressions have investigated the respective contribution of emotion processing and action-related brain areas. Studies clearly show that the AMY, a brain region associated with emotion processing (Phelps & LeDoux, 2005), is sensitive to the emotional significance of body movements (de Gelder, Hortensius, & Tamietto, 2012; Sinke, Sorger, Goebel, & de Gelder, 2010; Pichon, de Gelder, & Grezes, 2008; Grezes, Pichon, & de Gelder, 2007; Peelen & Downing, 2007) and modulates activity in body-selective areas (Peelen & Downing, 2007). This modulatory role of the AMY is consistent with research showing AMY's involvement in several component processes, such as stimulus appraisal, relevance detection, activation of neuroendocrine responses, and somatic motor expressions of emotion (Sander, Grandjean, & Scherer, 2005). Given its many connections to brain areas involved in behavioral output (Mosher, Zimmerman, & Gothard, 2010; Young, Scannell, Burns, & Blakemore, 1994), AMY is involved in assessing the relevance/significance of stimuli, signaling what is important in any particular situation, and then modulating the appropriate perceptual, attentional, autonomic, and cognitive/conceptual processes to deal with the challenges or opportunities that are present (Cunningham, Arbuckle, Jahn, Mowrer, & Abduljalil, 2010; Laine, Spitler, Mosher, & Gothard, 2009). Studies investigating the sensitivity of the extrastriate body area (EBA)/V5/MT to bodily emotional expressions have been inconclusive, with some evidence (van de Riet et al., 2009) suggesting that EBA is not sensitive to the emotion displayed and other (Peelen & Downing, 2007) indicating that EBA is sensitive to the emotional significance of body movements.

Despite a large amount of research on the neural systems involved in processing social cognition, just a few studies have examined how these regions are recruited when viewing social interaction scenes (Wagner, Haxby, & Heatherton, 2012; Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Sinke et al., 2010). This is important because, when viewing complex scenes involving social interactions, observers spontaneously attempt to make sense of what is happening during the social interaction (Wagner et al., 2012) by also engaging regions involved in mentalizing (Iacoboni et al., 2004), such as the medial pFC (Amodio & Frith, 2006; Mitchell, Cloutier, Banaji, & Macrae, 2006; Saxe, 2006; Gallagher & Frith, 2003). Mentalizing-related regions are also engaged when passively viewing social animations (Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Wheatley, Milleville, & Martin, 2007). Noteworthy, the majority of the research on the neural basis of social cognition has not provided a relevant social context nor involved behavioral measures to link with brain imaging data (Kujala, Carlson, & Hari, 2012; Hadjikhani & de Gelder, 2003). This is unlike what happens in everyday life, where people are typically involved in dynamic interactions with others in a defined social context that guides their interpretation of the mental and emotional states of the target (e.g., Aviezer et al., 2008; Kim et al., 2004) and ultimately the evaluation of others' attitudes and behaviors. To address this important issue, we selected two common types of social interactions, one involving approach and the other avoidance, and placed them in a socially relevant context (i.e., business setting).

The main goal of this study was to investigate the neural correlates of observing social interactions in which whole-body dynamic stimuli display approach and avoidance behaviors in a business setting, followed by participants' ratings of these behaviors. An important and understudied aspect of approach and avoidance social interactions is the role of handshake in the perception of the ensuing interaction. Handshake has been proven to increase the perception of trust and formality of the relationship (Burgoon, 1991), and handshake initiated by a female has been shown to increase the perceived feeling of security when making risky financial decisions (Levav & Argo, 2010). Despite its importance for peoples' emotional well-being, the study of interpersonal and emotional effects of handshake has been largely neglected. Therefore, another goal of this study was to investigate the effect of handshake as a way of formal greeting on the perception of approach and avoidance behaviors. To investigate these issues, fMRI data were recorded while healthy participants viewed movies of social interactions in which whole-body dynamic characters displayed approach and avoidance behaviors that were preceded or not by a handshake and were followed by ratings of competence, interest in doing business, and trustworthiness (see Figure 1). These ratings were employed to investigate brain–behavior relationships to elucidate the significance of common and differential engagement of the social cognition regions in perceiving and evaluating approach and avoidance behaviors. In addition, skin conductance recording was also employed to reveal the specific role of the AMY in these interactions.

On the basis of the extant evidence, we made the following three predictions. Concerning the behavioral results, we predicted greater ratings for approach than for avoidance behaviors and a positive effect of handshake on the evaluation of social interactions. Concerning the fMRI data, we predicted both common and dissociable activation of the social cognition network to approach and avoidance behaviors. For brain regions commonly involved irrespective of the type of social interaction, we predicted increased activity in emotion (AMY) and action-related areas (STS, EBA, inferior frontal gyrus [IFG]), as well as in mentalizing-related regions such as the medial pFC. For dissociable brain areas showing increased sensitivity to Approach, we expected that the inviting behaviors would be associated with increased motivational salience (Schiller, Freeman, Mitchell, Uleman, & Phelps, 2009; Cunningham, Van Bavel, & Johnsen, 2008), increased vigilance (Davis & Whalen, 2001) and assessments of others' goals possibly reflected in increased activity in the AMY and STS (Kujala et al., 2012), and for brain areas showing increased sensitivity to Avoid condition, we expected that the avoidant behaviors would lead to

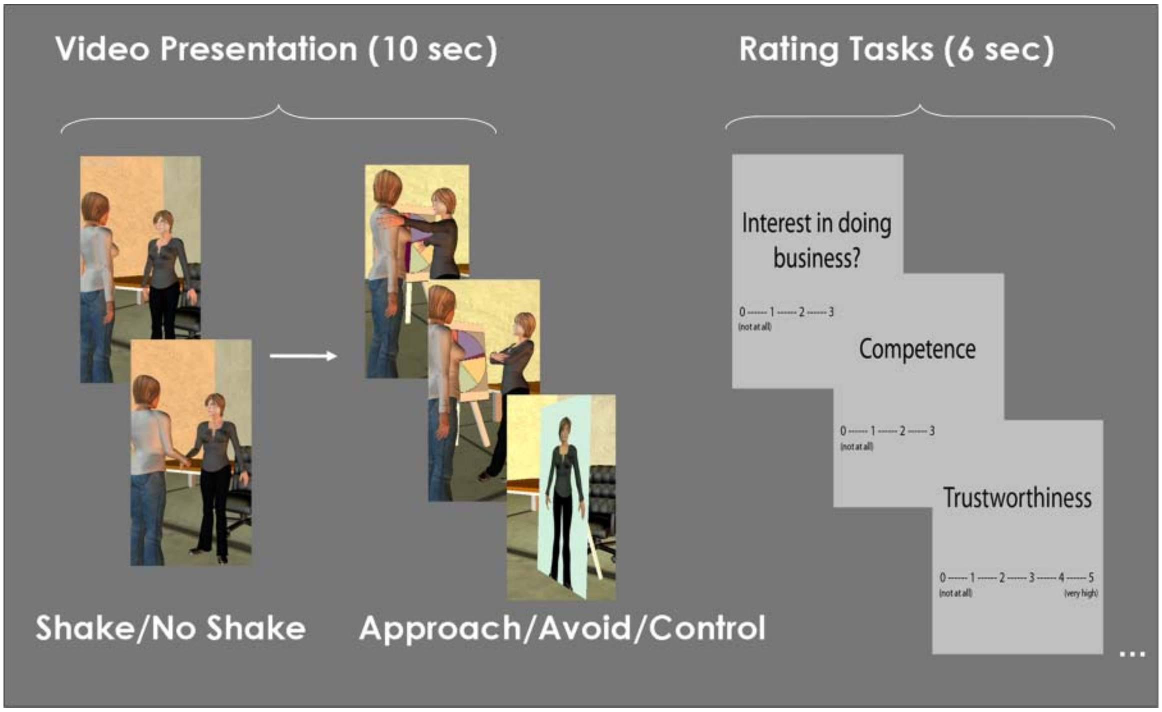

Figure 1. Diagram of the task. Event-related fMRI data were recorded while participants viewed videos of guest–host interactions, in which hosts displayed either behaviors inviting for further interactions (Approach) or discouraging further interactions (Avoid condition); unanimated hosts were also used as a no social interaction (Control) condition. Half of the social interaction trials were preceded by a handshake, and following the video viewing participants rated the hosts on Competence and Trustworthiness, and also rated their own Interest in doing business with hosts. Each 16-sec trial was followed by 8-sec intertrial intervals.

increased activity in early visual areas, such as cuneus (Kujala et al., 2012). Finally, linked to the positive effect of handshake on the evaluation of social behaviors, we performed exploratory analyses targeting the nucleus accumbens (NAcc), which is part of the reward pathways that have been linked to processing of appetitive rewards (Knutson & Greer, 2008) and of preference-related signals (Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007; O'Doherty, Buchanan, Seymour, & Dolan, 2006).

METHODS

Participants

Eighteen right-handed young healthy adults (18–34 years, nine women) participated in the study. Participants were native English speakers and had no history of neurological, psychological, or psychiatric illness. The experimental protocol was approved by the Health Research Ethics Board at the University of Alberta, and all participants provided written informed consent and received payment for their participation.

Experimental Design

Stimuli were created using Poser 7.0 (poser.smithmicro.com/poser.html) and presented using the CIGAL software (Voyvodic, 1999; www.nitrc.org/projects/cigal/). The task consisted of a series of 10-sec animated videos of nonverbal guest–host interactions in a business setting (Figure 1). Participants viewed the guest being greeted by a host (social interaction condition) or a cardboard cut-out of a host (no social interaction/control condition). The host displayed behaviors that were inviting to further social interaction (Approach condition) or behaviors that may indicate lack of interest in further interaction (Avoid condition); for a dynamic illustration of the stimuli, see Sung et al. (2011). Specifically, in the Approach condition, the hosts physically approached the guest by stepping toward him/her while displaying an "open/inviting" posture reflected in her open arms and smiling face. On the other hand, in the Avoid condition, the host stepped away while displaying a "closed/noninviting" posture reflected in crossed arms/legs and a grimace on her face. Moreover, there were two degrees of Approach and Avoidance behaviors: one "milder" and one "stronger." In the strong Approach condition, in addition to approaching the guest with an open posture, the host also friendly taps him/her on the shoulder, whereas in the strong Avoid condition, in addition to physically stepping away from the guest and displaying a closed posture, the host also sits indifferently on a chair. Although potentially interesting, dissociating between milder and stronger conditions was not the main focus of the present investigation; the main purpose of their inclusion was to maintain novelty in the stimulation throughout the study.

Within each condition, in half of the trials, the social interaction started with a handshake initiated by the host as part of the greeting protocol; the order of trials with and without handshakes was counterbalanced across participants. The timing of the actions was similar in the handshake and the no-handshake trials, in both the Approach and Avoidance conditions, which started at the same time. Also, the handshake itself was part of a greeting behavior, which was present even in the absence of the handshake behavior per se. To account for the overall biological motion that occurred during the Handshake condition, the host performed other greeting-related motions during the No-handshake condition, and therefore, the Handshake and the No-handshake conditions had overall comparable amounts of motion. To verify that the amount of movement across our conditions did not vary significantly, we measured the average luminance change between adjacent frames, by computing the absolute difference between each corresponding pixel in each neighboring frame and then averaging these values to a single score representing the change in luminance from one frame to another (Grezes et al., 2007). This strategy is in line with prior studies (Peelen & Downing, 2007) that have well documented the calculation of the variation in light intensity as a means to estimate the quantitative differences in movement in dynamic stimuli and ensure consistency across different conditions (Kret, Denollet, Grèzes, & de Gelder, 2011; Kret, Pichon, Grezes, & de Gelder, 2011; Pichon, de Gelder, & Grèzes, 2009; Pichon et al., 2008). Using this measure as an estimate of motion in the movies, overall and in specific chunks of frames when the hosts displayed behaviors that were clearly indicative of Approach and Avoid conditions, averages of changes in luminance were calculated for each condition on a frame-by-frame basis (30 frames/sec). These averages were then used to test for differences in the quantity of movement between the two types of social interactions, as well as compared with the control condition. Videos were followed by rating screens asking the subject to rate the host on competence, trustworthiness, and interest in doing business on a 6-point Likert scale (0 = *not at all*/5 = *very much*); these ratings were counterbalanced across trials.

Characters in videos were equated for the displayed behavior (Approach vs. Avoidance), ethnic background (White vs. Non-White), shirt color, and hairstyle. The guest characters were men in half of the trials and women in the other half, and their gender was randomly alternated between trials. On the basis of previous evidence showing that physical contact with female hosts, such as handshake or gentle touch on the shoulder, may influence business-related decisions (Levav & Argo, 2010), in our study, all hosts were women. Also, a handshake initiated by a woman seems to lead to an increased feeling of security (Levav & Argo, 2010) and increased ratings of relaxation (Burgoon, 1991). Although in North American culture (including in business and academic settings) a handshake is customary for both women and men when making new acquaintances, gender or cultural differences may exist in the initiation and use of different types of formal greetings, such as handshake or bowing; these are interesting issues that warrant further investigation (Kret & de Gelder, 2012). Depending on the sex of the guest, the subjects were also asked to take either the first (ME) or third (OTHER) person perspective in observing the social interactions, with the perspective taken being cued before the beginning of each trial—that is, for guest characters of the same sex as their own, subjects were prompted to take the ME perspective, whereas before each trial with a guest of a different gender, the subjects were prompted to take the OTHER perspective. Although comparison between first- and third-person perspectives is important in social cognition (Wagner et al., 2012), this was not the focus of the present investigation, as the main goal was to examine the effects of Approach and Avoidance behaviors, preceded or not by a handshake. It would, nevertheless, be interesting to investigate this issue in future studies also including male hosts and involving larger numbers of trials.

Participants completed 6 runs/blocks of 16 trials each for a total of 96 trials, identified based on the condition (32 approach, 32 avoidance, and 32 control); different run/block orders were randomly assigned to the participants. To avoid induction of long-lasting effects states, the trials within each block were pseudorandomized so that no more than three trials of the same type were consecutively presented. Before performing the task, subjects were instructed to use the whole rating scale and to make the ratings based solely on the social interaction that was being shown, as well as to make quick and accurate responses. Each run started with 6 sec of a fixation to allow stabilization of the fMRI signal. An intertrial interval of 8 sec followed each movie trial and ended each run. To investigate the link between basic physiological responses and activity in targeted brain regions (i.e., the AMY), skin conductance responses were also measured in all subjects throughout the task, using a BIOPAC system (www.biopac.com/). Data were recorded and analyzed using Acknowledge and MATLAB to detect differences in sympathetic responses linked to observing and rating the stimuli.

Skin Conductance Recording and Analysis

MRI-compatible electrodes (EL507, BIOPAC, Goleta, CA) were attached to the palmar surface of the distal phalanges of subjects' left index and middle fingers. Participants were instructed not to move that hand during the duration of the study. While subjects performed the rating task, skin conductance response was processed through a skin response amplifier (GSR100C, BIOPAC was used with a Gain of 5 $\mu\mho$/V and a 1.0 Hz low pass filter) and recorded digitally using the BIOPAC Acqknowledge software. A phasic signal was extracted (with a 0.05 Hz high pass filter) from the recorded tonic signal. The resulting data were then selectively averaged (using 16 sec epochs) and separated by trial type. Analyses of changes in the skin conductance data linked to changes in the fMRI signal focused on responses associated with the time of approach or avoid social interactions displayed by the host characters in the movies.

Neuroimaging Protocol

MRI data were recorded using a 1.5-T Siemens Sonata scanner. The anatomical images were 3-D MPRAGE anatomical series (repetition time [TR] = 1600 msec, echo time = 3.82 msec, field of view = 256 × 256 mm, number of slices = 112, voxel size = 1 × 1 × 1 mm) and the functional images consisted of series of images acquired axially using an echoplanar sequence (TR = 2000 msec, echo time = 40 msec, field of view = 256 × 256 mm, number of slices = 28, voxel size = 4 × 4 × 4 mm), thus allowing for full-brain coverage. Stimuli were projected on a screen directly behind the participant's head within the scanner, which participants viewed through a mirror. Responses were recorded using a four-button response box placed under the participant's right hand; extreme ratings (0 = *not at all* and 5 = *very much*) were indicated by the participants with double clicks on Buttons 1 and 4, respectively.

Data Analysis

Behavioral Data Analysis

Differences in ratings for competence, interest in doing business, and trustworthiness between the approach and avoidance behaviors and differences in ratings between the Handshake and No-handshake interactions were assessed using repeated-measures ANOVAs.

fMRI Data Analysis

Statistical analyses, performed with SPM2 (Statistical Parametric Mapping), were preceded by the following preprocessing steps: quality assurance, TR alignment, motion correction, coregistration, normalization, and smoothing (8 mm^3 kernel). Individual analyses produced whole-brain activation maps for the contrasts of interest (e.g., Approach vs. Control, Avoidance vs. Control, Approach vs. Avoidance), which were used as inputs for second-level random effects group analyses. The SPM analyses were complemented by analyses that allowed extraction of the fMRI signal, for display purposes and further investigations, which were performed with in-house MATLAB tools. All the analyses related to the main focus of the investigation focused on effects time-locked to the moment of social interaction, when the hosts displayed approach or avoidance behaviors. The exploratory analyses investigating the effect of handshake on activity in the NAcc and further exploring effects identified at the time of Approach/Avoid actions focused on responses time-locked to the moment when the Handshake occurred.

The main goal of the study was to investigate the neural correlates of observing social interactions, in which whole-body dynamic stimuli displayed approach and avoidance behaviors in a socially relevant context (i.e., a business setting), followed by participants' ratings of these behaviors. The focus was on the role of regions from the social cognition network. To accomplish this goal, analyses were performed to identify the common set of brain regions whose activity was sensitive to the presence of both approach and avoidance social interaction, through conjunction analyses. The effect of social interaction was measured as greater activity (compared with control) for social interaction stimuli (approach and avoidance interactions) than for nonsocial interaction stimuli (static bodies). This was done by identifying regions that showed both (i) greater activity for approach than for control movies and (ii) greater activity for avoidance than for control movies. Then, the conjunction map identifying social interaction effects that were common to both approach and avoidance was defined as ([Approach > Control] ∩ [Avoidance > Control]) and calculated using the ImCalc feature in SPM. Also subserving the main goal, analyses were performed to identify dissociable sets of brain regions showing greater sensitivity to Approach or to Avoidance conditions by measuring significant bidirectional differences between approach and avoid trials (i.e., Approach > Avoidance and Avoidance > Approach). For these whole-brain analyses, the statistical maps were corrected for multiple comparisons using the false discovery rate (FDR) correction (Genovese, Lazar, & Nichols, 2002). For analyses comparing social interactions versus control trials (Approach > Control and Avoidance > Control), a threshold of $p < .005$ FDR-corrected was used, and for the direct contrasts between approach and avoidance conditions (Approach > Avoidance and Avoidance > Approach), a threshold of $p < .05$ FDR-corrected was used. Analyses investigating whole-brain patterns of activation described above were complemented by analyses focusing on an a priori ROI, which included the AMY (Dolcos, LaBar, & Cabeza, 2004). For these analyses investigating our a priori hypotheses regarding the responses in the AMY, a threshold of $p < .05$ uncorrected and an extent threshold of five contiguous voxels was used. A threshold of 10 contiguous voxels was used in the rest of the brain. Finally, to further elucidate the role of the brain regions showing common or dissociable engagement in response to approach and avoidance behaviors, brain–behavior relationships were investigated by examining covariations of their responses with behavioral ratings and skin conductance. Behavioral and physiological measures were correlated with mean statistics after identifying clusters of activation. Finally, for the exploratory analyses investigating the effect of handshake as a way of formal touch (e.g., NAcc), a threshold of $p < .05$ uncorrected, and an extent threshold of five contiguous voxels was used. Given that analyses involved normalization to a template and smoothing, as typically performed for whole-brain analyses, defining structures based on stricter anatomical landmarks similar to our previous studies (e.g., Dolcos et al., 2004) was not necessary; hence, all activations were defined at the group level.

RESULTS

Behavioral Results

Higher Ratings for Approach than for Avoidance Behaviors and Positive Impact of Handshake on the Evaluation of Social Interactions

As predicted, ratings for competence, interest in doing business, and trustworthiness were all higher for the Approach ($M = 3.31/3.38/3.38$, $SD = 0.51/0.54/0.66$) than for the Avoidance ($M = 2.52/2.22/2.42$, $SD = 0.72/0.94/0.78$) condition (Figure 2A). This effect was confirmed by a repeated-measures ANOVA, showing a significant main effect of Social Interaction on the ratings for Approach and Avoidance conditions: $F(1, 17) = 23.29$, $p < .001$, $\eta^2 = 0.58$; post hoc paired t tests showed that this difference was significant for all three ratings: Competence ($t(17) = 4.08$, $p < .001$), Interest ($t(17) = 4.98$, $p < .001$), and Trustworthiness ($t(17) = 4.46$, $p < .001$). Regarding the effect of Handshake, as predicted it increased the ratings in both Approach and Avoidance behaviors (Figure 2B). This effect was confirmed by a significant main effect of Handshake, $F(1, 17) = 34.85$, $p < .001$, $\eta^2 = 0.67$, which affected both the Approach (Handshake: $M = 3.72$, $SD = 0.68$, No Handshake: $M = 2.99$, $SD = 0.51$, $t(17) = 5.71$, $p < .001$) and the Avoidance (Handshake: $M = 2.64$, $SD = 0.89$, No Handshake: $M = 2.13$, $SD = 0.73$, $t(17) = 5.15$, $p < .001$) conditions. Interestingly, the effect of Handshake was stronger in the Approach than in the Avoidance condition, as shown by a significant interaction between Handshake × Social Interaction, $F(1, 17) = 5.75$, $p < .05$, $\eta^2 = 0.25$. Overall, these findings show that our behavioral manipulation worked in producing more positive evaluations of the host when displaying behaviors that encourage further social interactions and that physical touch in the form of a handshake preceding the actual social interactions increases the positive impressions and attenuates the negative ones.

Brain Imaging Results

Common and Dissociable Engagement of the Social Cognition Network by Approach and Avoidance Behaviors

Regarding the common brain areas involved irrespective of the type of social interaction, conjunction analyses revealed a set of regions (see Figure 3 and Table 1) that responded more strongly to movies of social interaction (both Approach and Avoidance) than to movies with no social interaction (Control). As predicted, these brain regions included areas that are part of the social cognition network, such as the posterior STS (bilaterally, with a rightward asymmetry and extending into surrounding areas, such as the middle temporal gyrus [MTG], in the left hemisphere, and the TPJ and EBA, in the right hemisphere), the medial pFC, the lateral pFC (bilaterally, with a rightward asymmetry, mainly covering the IFG and extending into the middle frontal gyrus), and the right AMY. In addition, bilateral caudate and the right inferior parietal lobule were also commonly activated by both approach and avoidance behaviors.

Correlation analyses showed that brain activity in some of these common regions also covaried with behavioral ratings for Approach or Avoid conditions. In the

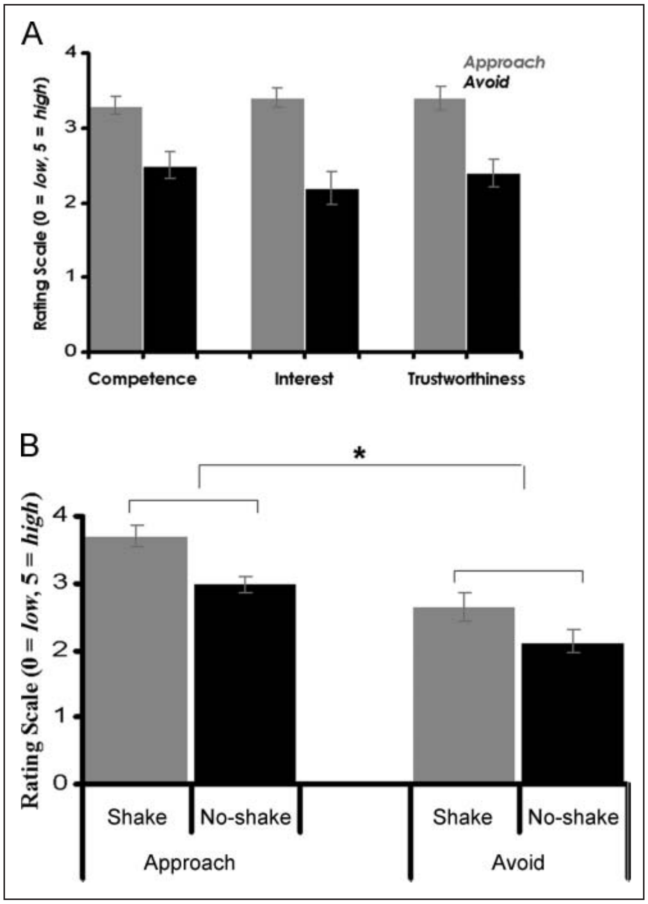

Figure 2. Higher ratings for Approach than for Avoidance and for Handshake than for No-handshake Social Interactions. (A) Higher ratings for Approach than for Avoid interactions are confirmed by a significant main effect of Social Interaction on the ratings for Approach and Avoid conditions and by paired comparisons of the rating scores; this difference was observed systemically for all three ratings. (B) Higher ratings for Handshake than for No-handshake interactions were confirmed by a significant main effect of Handshake on the ratings for Approach and Avoid conditions. Moreover, the effect of Handshake was stronger in the Approach than in the Avoid condition, as confirmed by a significant ANOVA interaction between Handshake × Social Interaction conditions. * denotes significance of the interaction. The error bars denote standard errors of means.

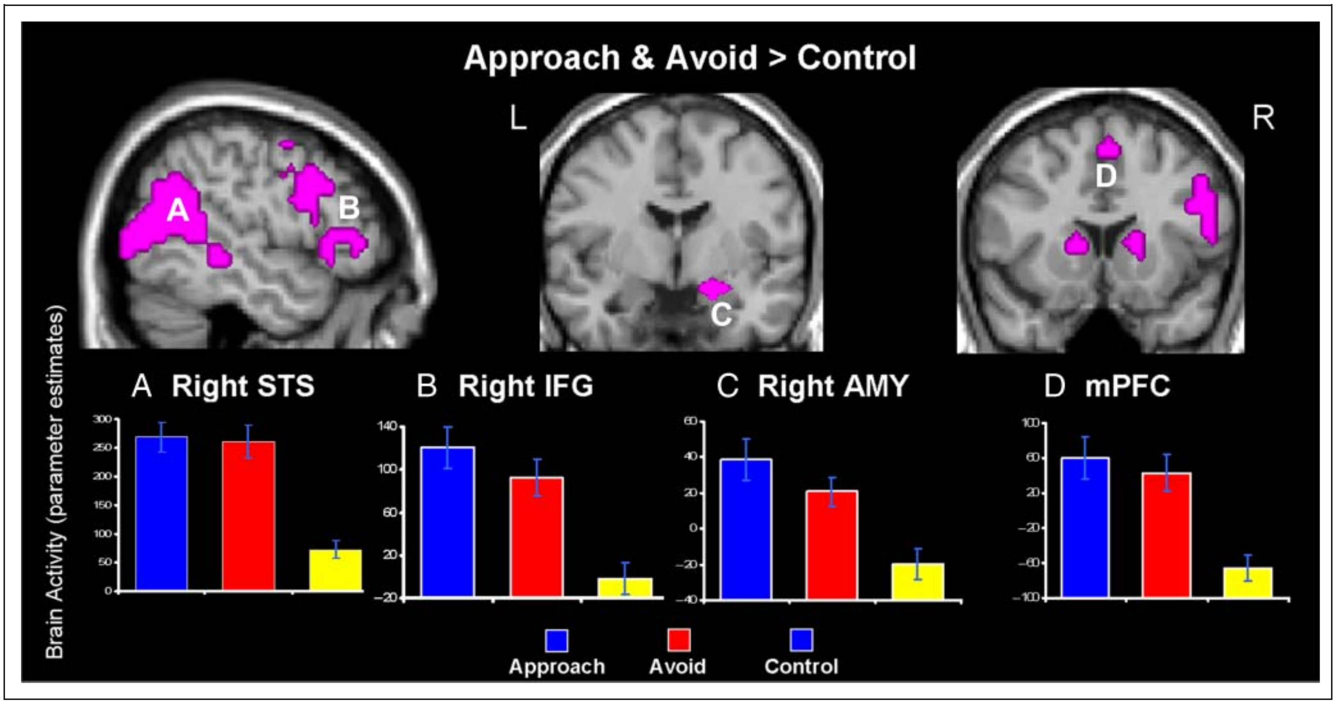

Figure 3. Common engagement of the social cognition network by Approach and Avoid behaviors. The activation maps displayed in magenta identify brain regions (A: Right STS; B: Right IFG; C: Right AMY; D: mPFC) showing greater response to social interaction (both Approach and Avoid) trials than to Control trials, time-locked to the onsets of approach/avoidance behaviors. The "activation maps" are superimposed on high-resolution brain images displayed in lateral (left) and coronal (middle and right) views. The bar graphs illustrate the corresponding contrast estimates, as extracted from representative peak voxels from the regions illustrated. The error bars denote standard errors of means. mPFC = medial pFC; L = left; R = right.

Approach > Control contrast, the left MTG ($x = -44$, $y = -73$, $z = 11$, BA 39) and the right inferior parietal lobule ($x = 40$, $y = -53$, $z = 36$, BA 40) were positively correlated, whereas the right inferior parietal lobule ($x = 51$, $y = -45$, $z = 28$, BA 40) was negatively correlated with the ratings for Approach. In the Avoid > Control contrast, the right MTG ($x = 48$, $y = -42$, $z = 6$, BA 22), the right middle occipital gyrus ($x = 44$, $y = -74$, $z = 4$, BA 19), and the right IFG ($x = 51$, $y = 35$, $z = 2$, BA 45, and $x = 51$, $y = 9$, $z = 29$, BA 9) were negatively correlated with the ratings for Avoid.

Regarding the brain areas showing greater sensitivity to Approach or to Avoid conditions, analyses involving their direct comparisons identified brain regions showing dissociable responses to the associated trials (Table 1). As predicted, the Approach > Avoid contrast revealed that the left STS, the right medial frontal areas, and bilateral AMY, along with bilateral parietal regions, responded more strongly to approach than to avoidance behaviors. The reverse contrast (*Avoid* > *Approach*) identified only an area in the visual cortex (cuneus), which responded more strongly to *Avoid* than to *Approach* behaviors.

Correlation analyses showed that brain activity in some of these dissociating regions also covaried with behavioral ratings. Specifically, activity in the left superior parietal lobule ($x = -28$, $y = -60$, $z = 40$, BA 7) and the left AMY correlated positively with the ratings for Approach; the latter will be discussed in detail below.

Increased AMY and STS Response Linked to the Positive Evaluation of Approach Behavior and Positive Impact of Handshake

Covariations of activity in the AMY with the behavioral ratings and skin conductance responses further elucidated the role played by this region in the positive evaluation of approach behaviors (Figure 4). Specifically, the left AMY was positively correlated with Competence and Interest ratings for *Approach* (Talairach coordinates: $x = -20$, $y = -5$, $z = -13$), whereas the right AMY was positively correlated with the Competence ratings for Approach (Talairach coordinates: $x = 12$, $y = -5$, $z = -13$). Noteworthy, these areas overlapped partially with the AMY regions that overall showed increased response to approach than to avoidance behaviors. Regarding the covariations with skin conductance data, these analyses identified that activity in right AMY showing greater overall response to Approach than to Avoidance also correlated negatively with skin conductance responses to approach but not to avoidance conditions (Talairach coordinates: $x = -20$, $y = -1$, $z = -17$). Overall, these findings suggest that greater activity in the AMY to Approach than to Avoid behavior reflect a positive evaluation of the Approach behavior.

Table 1. Common and Dissociating Brain Regions Involved in the Evaluation of Approach and Avoid Behaviors

			Talairach Coordinates			*t*	
Brain Region	*BA*	*H*	*x*	*y*	*z*	*Approach > Control*	*Avoid > Control*
Approach and Avoid > Control							
AMY	34	R	12	−5	−13	5.48	4.78
Superior temporal gyrus	40	L	−51	−49	21	8.43	6.46
	22	R	48	−57	18	15.23	10.65
	22	R	51	46	13	8.99	11.43
MTG	39	L	−44	−73	11	9.22	8.89
	39	L	−40	−61	18	8.87	7.22
Supramarginal/inferior parietal lobule	40	R	48	−45	28	9.5	6.36
Medial superior frontal gyrus	8	R/L	0	18	51	5.93	5.66
IFG	47	L	−44	23	−5	5.67	5.47
	45	L	−48	20	3	5.7	4.54
	9	R	51	9	29	9.29	6.54
	45	R	51	35	2	7.97	5.81
Middle frontal gyrus	6	R	44	2	48	8.14	5.11
	9	R	48	17	32	8.58	5.86
	6	R	36	−1	55	8.11	5.02
Caudate nucleus		L	−16	12	7	5.89	6.39
		R	12	16	7	6.97	6.16
Middle occipital gyrus/EBA	19	R	48	−73	7	7.11	7.18
Approach > Avoid							
AMY	34	R	16	−1	−17	2.84*	
	34	L	−20	−5	−17	3.09*	
Superior temporal gyrus	22	L	−55	−58	14	5.27	
Inferior parietal lobule	40	L	−59	−37	46	7.11	
	40	L	−44	−37	42	5.7	
	40	L	−52	−33	38	4.84	
	40	L	−36	−48	58	6.13	
	40	R	35	−37	39	4.18	
Superior parietal lobule	7	L	−28	−56	40	5.61	
Precuneus	7	R	28	−44	46	5.33	
Medial frontal gyrus	9	R	8	37	31	4.85	
Cingulate gyrus	32	R	12	25	28	4.21	
Avoid > Approach							
Cuneus	17	R	8	−77	11	7.22	

A threshold of $p < .005$ FDR-corrected was used for analyses comparing social interactions versus control trials (i.e., Approach > Control and Avoidance > Control), and a threshold of $p < .05$ FDR-corrected was used for the direct contrasts between Approach and Avoidance conditions (Approach > Avoidance and Avoidance > Approach).

BA = Brodmann's area; H = hemisphere; R = right; L = left.

*Significant at $p < .05$, uncorrected.

Further investigation of the time course of activity in the left pSTS revealed that increased response in this region to approach compared with avoidance behaviors, time-locked to the time of the actual display of approach behavior, was driven by the Approach trials preceded by a handshake. Specifically, trials with a handshake preceding the social interaction also activated (although at a lower threshold of $p < .005$, uncorrected) the same area of the left pSTS that later on responded more strongly to Approach than to Avoidance behaviors (Figure 5). This finding suggests a link between the initial evaluation of handshake and subsequent increased pSTS response to and ratings of approach compared with avoidance behaviors and point to a possible role of this pSTS area in the positive impact of handshake on behavioral ratings. Finally, similar exploratory analyses comparing the fMRI response time-locked to the time when the handshake took place (i.e., the Handshake vs. No Handshake contrast) revealed that the right NAcc responded more strongly to the greetings including a handshake than to those without it.

It should be noted that there were no differences in the mean scores reflecting the overall amount of motion between the Approach and Avoid conditions (Approach: $M = 2.96$, $SD = 4.62$; Avoid: $M = 2.81$, $SD = 4.47$, two-tailed t test $p = .68$) nor between the frames in which the Approach and Avoid actions actually occurred (Approach: $M = 3.12$, $SD = 5.73$; Avoid: $M = 2.91$, $SD = 5.55$; two-tailed t test $p = .76$). Noteworthy, although in the Control condition there was no motion displayed by the hosts, there were no significant differences between the Approach and Avoid compared with the Control trials ($M = 2.79$, $SD = 5.24$; two-tailed t test $p = .67$, .96, respectively). This similarity in motion between the social interaction and the control trials was created by increased panning in the latter, which seemingly contributed to changes in luminance as much as the biological motion observed in the social interaction conditions. Finally, comparison of motion on a frame-by-frame basis during the time interval when the Handshake or other greeting motions occurred did not identify statistically significant differences between the Handshake and No-handshake conditions ($p = .27$).

DISCUSSION

A growing body of literature demonstrates the implication of regions of the social cognition network in mental inferences about encountered individuals. This study contributes to this literature by addressing important missing

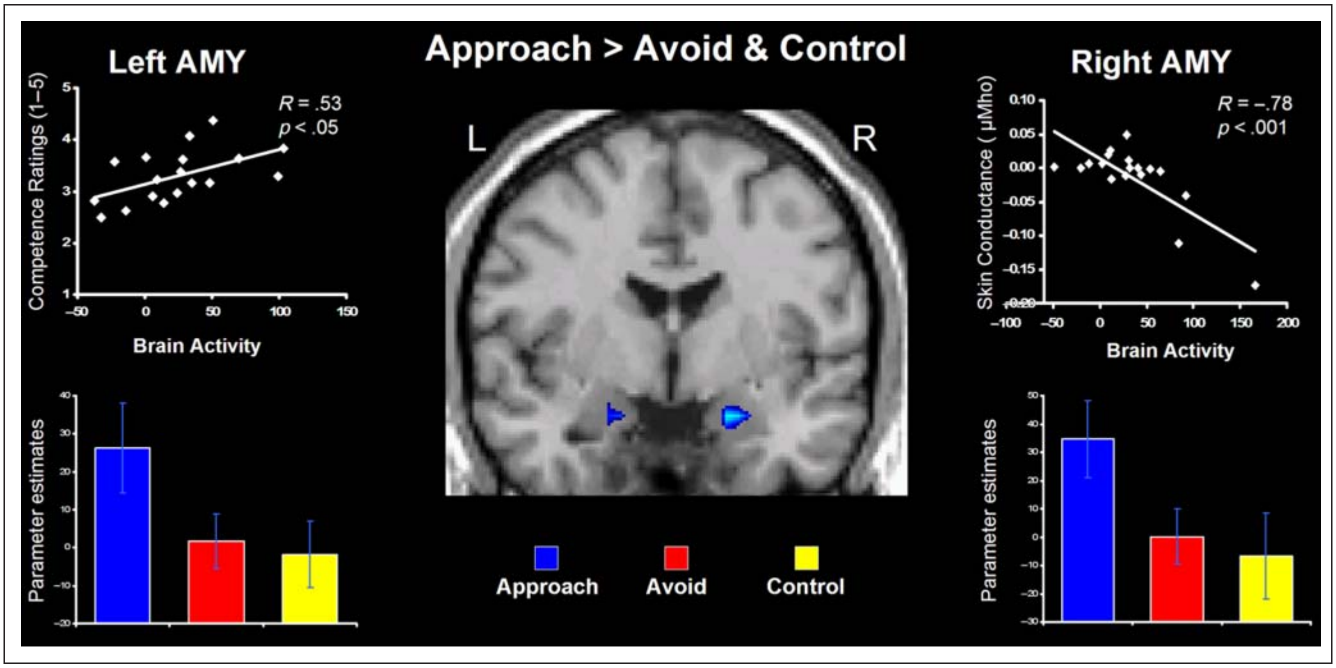

Figure 4. Increased activity in the AMY linked to positive evaluation of Approach behavior. Analyses elucidating the significance of increased AMY response to approach compared with avoid behaviors identified positive correlations with behavioral ratings (bilateral AMY) and negative correlations with skin conductance (right AMY). The central panel illustrates the activation map showing overall greater brain activity to Approach than to Avoid trials, time-locked to the onsets of approach/avoid behaviors, superimposed on a high resolution brain image displayed in coronal view. The scatterplot on the left side illustrates the correlation identified in the left AMY for Competence ratings; similar effects in the left AMY were found for the Interest ratings and also in the right AMY for the Competence ratings. The scatterplot on the right side illustrates the correlation identified in the right AMY for skin conductance responses. The bar graphs illustrate the corresponding contrast estimates for the same AMY peak voxels as those illustrated in the correlation scatterplots. Overall, these findings are consistent with an interpretation favoring a positive evaluation of approach behavior linked to the overall increased AMY response to Approach compared with Avoid behaviors. The error bars denote standard errors of means. L = left; R = right.

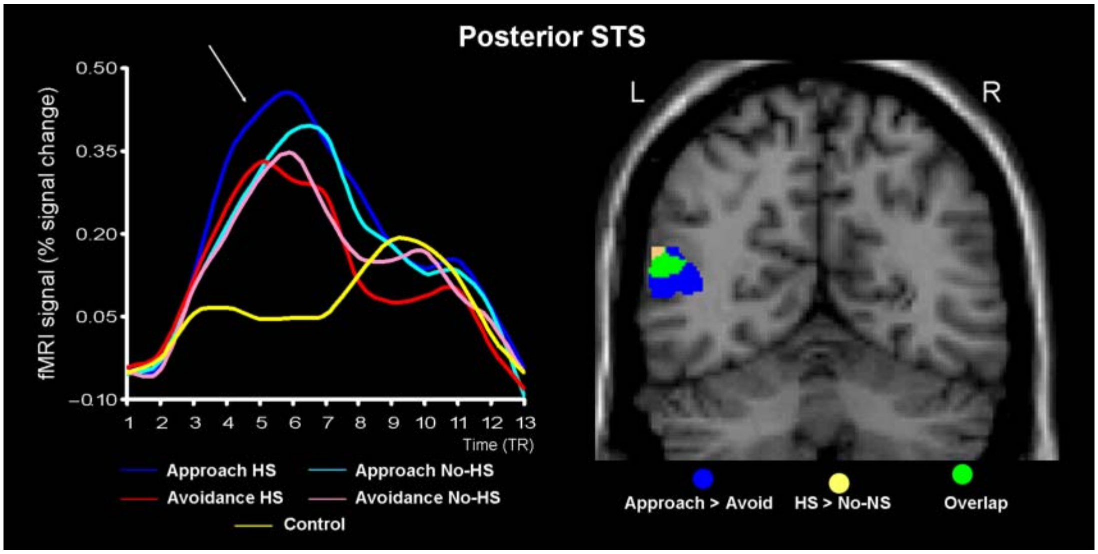

Figure 5. Handshake preceding social interaction activated the same area of the left pSTS that later on responded more strongly to Approach than to Avoid behavior. The activation maps on the right side panel, reflecting brain activity time-locked to the onsets of approach/avoidance behaviors, are superimposed on a high-resolution brain image displayed in a coronal view. For illustration purposes, the Approach vs. Avoid activation (blue blob) is displayed at a threshold of $p < .005$, uncorrected. The line graph in the left side panel illustrates the time courses of the fMRI signal, extracted from the whole ROI meeting the conjunction criteria (green blob), for each trial type and TR (1 TR = 2 sec). As indicated by the arrow, greater response for Approach than for the Avoid condition was driven by the Approach trials preceded by a handshake. L = Left; R = Right; STS = superior temporal sulcus; HS = handshake; No-HS = no handshake.

elements regarding the effect of approach and avoidance behaviors displayed by partners interacting in a relevant social context (i.e., a business setting). Three novel findings emerged from this investigation, helping to elucidate the effect of approach and avoidance social interactions and handshake on evaluative responses of encountered individuals and their associated neural correlates. First, approach was associated with more positive evaluations than avoidance social interactions, and handshake preceding social interaction enhanced the positive effect of approach and diminished the negative effect of avoidance on the evaluation of social interactions. Second, common and dissociable brain regions from the social cognition network were involved in the evaluation of approach and avoid social interactions. Third, increased sensitivity to approach than to avoidance in AMY and STS were linked to the positive evaluation of the approach behavior and positive impact of handshake, and linked to the overall positive effect of the handshake on social evaluation, there was greater activity in the NAcc for the handshake than for the no-handshake condition. These findings will be discussed in turn below.

Higher Ratings for Approach than for Avoidance Behaviors and a Positive Effect of Handshake on the Evaluation of Social Interactions

Traditionally, studies investigating approach–avoidance behaviors have mainly focused on the experience or the response of observers to approach or avoidant behaviors conveyed by static stimuli, most often faces (e.g., Harmon-Jones, 2003; Cacioppo, Priester, & Berntson, 1993). However, the implied approach–avoidance tendencies attributed to expressive static faces and gestures are not always equivalent to the approach–avoidance reactions elicited by them when actually displayed in motion (Adams, Ambady, Macrae, & Kleck, 2006) and in a specified context. In this study, we focused on the effect of expressive dynamic whole-body human gestures displaying approach and avoidance behaviors, which are the most fundamental form of behavioral intention (Adams et al., 2006), on the evaluation of the person displaying that behavior. Our results suggest that other peoples' body signals reflecting approach or avoidance intentions play a critical role on evaluative judgments in a business-like setting. The spontaneous impression that people form about a social interaction partner influences their trustworthiness and competence evaluations and, ultimately, their interest to pursue future business interactions with that partner.

Turning to the effect of handshake, interpersonal touch provides an often overlooked channel of communication (Hertenstein, 2002). Through repeated social interactions, people become able to decode distinct emotions and behavioral intentions when they are touched by another person. For example, in the United States, stroking and patting are commonly perceived as reflecting sympathy and shaking of the hand as reflecting gratitude (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006). Also, the formal handshake as part of the initial greeting in social interactions is known to increase the perceptions of trust and feelings of security (Levav & Argo, 2010; Burgoon, 1991). Our results showing increased ratings for both approach and avoidance behaviors confirmed the favorable effect of a handshake in a social interaction. The present investigation also expanded previous studies by showing that a simple handshake at the beginning of a social interaction has a favorable effect on evaluations of competence, trustworthiness, and interest to pursue future business interactions. Furthermore, it also showed that a handshake enhanced the evaluation of approach behavior more so than of avoidance behavior. It is possible that, because the positive expectations established by the preceding affective handshake were more congruent with the nonverbal communication displayed later in the approach behaviors, it resulted in an enhanced positive effect of approach behaviors. The diminished negative impact of avoidance behavior by handshake is also important, as it suggests that formal touch preceding social interactions can reduce the impact of negative impressions. As discussed below, these positive effects of handshake observed behaviorally were linked to changes in the NAcc activity at the time of shake and in the left pSTS activity at the time of displaying approach/avoidance social interactions.

Common and Dissociable Engagement of the Social Cognition Network by Approach and Avoidance Behaviors

The observation of a whole-body dynamic social interaction, irrespective of its type, activated a common set of brain regions of the social cognition network, including the pSTS, the EBA, the pFC, and the AMY, more than watching whole-body static cardboards used as control conditions. These regions have been previously shown to be involved in perceiving single human stimuli (Downing, Wiggett, & Peelen, 2007; Grossman & Blake, 2002; Allison, Puce, & McCarthy, 2000; Haxby, Hoffman, & Gobbini, 2000), as well as in the observation of still and dynamic whole-body images of social interaction (Kujala et al., 2012; Centelles et al., 2011; Peelen & Downing, 2007), enabling perceivers to make mental inference about encountered individuals (Adolphs, 2009; Spreng, Mar, & Kim, 2009; Frith, 2007). Thus, overall these findings replicated previous reports that identify activity in regions of the social cognition network that evaluate the action intentions and emotions associated with nonverbal behaviors in social contexts. In addition, by further examining brain–behavior relationships and by linking their responses with measures of basic physiological responses (i.e., skin conductance) and/or by directly comparing approach and avoidance behaviors, the present report expands the extant evidence by providing further clarification of the role of specific regions in interpersonal evaluations of approach and avoid social interactions.

Increased AMY and STS Response Linked to the Positive Evaluation of Approach Behavior and Positive Impact of Handshake

This study also provided evidence clarifying the role of the AMY and pSTS in assessing nonverbal social interactions. First, we identified increased response in these regions to approach compared with avoidance behaviors. These results confirm previous findings showing increased AMY and pSTS activations to static pictures of people facing each other compared to facing away from each other (Kujala et al., 2012). Importantly, this study also expands previous findings by providing further clarification of the significance of these differences. In the case of the AMY, by linking the overall response in the fMRI signal to behavioral evaluations and autonomic responses elicited by observing dynamic approach and avoidance interactions, we provided evidence that increased activity to approach behavior was associated with a positive evaluation of these behaviors. Specifically, the AMY was correlated positively with the behavioral ratings and negatively with the skin conductance responses to approach but not to avoidance conditions.

These findings are consistent with a role of the AMY in positive evaluations of approach behaviors and identify a hemispheric asymmetry linked to individual differences in behavioral ratings (left AMY) and skin conductance responses (right AMY). Given the evidence concerning the role of the AMY in processing emotional arousal (Winston, Gottfried, Kilner, & Dolan, 2005; Anderson et al., 2003; Dolcos, Graham, LaBar, & Cabeza, 2003) and allocating attention to stimuli of importance (Adolphs, 2010; Roesch, Calu, Esber, & Schoenbaum, 2010; Holland & Gallagher, 1999), it is possible that greater activity to approach behavior reflects increased physiological arousal and a state of preparedness in response to approaching strangers. This interpretation is also consistent with evidence pointing to a relation between attention and AMY activation (de Gelder et al., 2012), supporting the vigilance account of AMY's function (Davis & Whalen, 2001; Whalen, 1998), and overall with the possibility that increased AMY activity could reflect a response signalling the need for further, more elaborate processing of the approach behavior. On the other hand, given the evidence concerning the AMY's role in processing positive emotions, it is possible that increased response to approach versus avoid behaviors is linked to a positive evaluation of approach behavior, which was also reflected in greater ratings to approach than to avoid behaviors. Overall, the present findings are consistent with both accounts and suggest that increased response to approach behaviors reflect the need to further evaluate the intentions of the characters displaying them, but this evaluation leads to

(i) reduced physiological arousal rather than increased (as reflected in the negative covariation of right AMY activity with skin conductance response) and to (ii) positive evaluation of approach behavior (as reflected in the positive covariation of the AMY activity with behavioral ratings).

Turning to the pSTS, the present findings suggest an involvement of this region in the positive impact of handshake on the positive evaluation of nonverbal behavior. Noteworthy, the increased response in this region to approach versus avoidance behaviors overlapped with areas showing increased response to the handshake behavior displayed before the actual display of approach behaviors. This suggests a link between the initial involvement of the pSTS at the time of handshake with its subsequent involvement in the assessment of approach behavior. Further investigation of activity in this region confirmed this idea by showing that the difference between approach and avoidance behaviors was driven by the trials preceded by a handshake (see Figure 5), which paralleled the behavioral pattern observed in the rating data, showing greater impact of handshake on approach compared with avoid behaviors (see Figure 2B). This interpretation provides a possible explanation for increased pSTS activations identified in studies involving static pictures of people posing approach (facing each other) versus avoid (facing away from one another) behaviors (Kujala et al., 2012), where closer physical proximity of the former behavior might have been more likely associated with the possibility of implied physical contact compared with the later behavior. Unlike other studies, however, where neither actual physical touch nor behavioral ratings were involved, here we provide evidence linking the response in the left pSTS with a positive impact of the handshake, as a formal way of physical touch, on the subsequent evaluation of approach behaviors.

The pSTS findings are also consistent with evidence from studies involving actual and observed physical touch (Gordon et al., in press; Ebisch et al., 2011), which identified increased STS activity to haptic stimulation. Such studies involved fMRI recordings while haptic stimulation was applied to participants' skin (e.g., hand) or during observation of different types of touch and found that, among other brain regions, both actual and observed physical touch were also associated with increased activity in the pSTS. These findings were interpreted as reflecting processing associated with comforting experience of being touched, which is mediated by CT fibers (Gordon et al., in press) and may be involved in the effect produced by physical touch in parent–infant or in romantic interactions. Given the evidence that handshake has been proven to increase the perception of trust and formality of the relationships (Burgoon, 1991), as well as the perceived feeling of security when making risky financial decisions (Levav & Argo, 2010), it is possible that the effects observed here may involve similar mechanisms that may also be involved in formal touch. Notable, though, it seems that only the mere observation of others' handshake as involved in present study, as opposed to actual handshake, may be enough to engage these mechanisms.

Our exploratory analysis also showed that the favorable effect of handshake on the evaluation of subsequent social interactions was associated with greater NAcc activity, time-locked to the moment when handshake occurred. The NAcc is a central component of the reward pathways and has been linked to processing of appetitive rewards (Knutson & Greer, 2008) and of preference-related signals (Haber & Knutson, 2010; Knutson et al., 2007; O'Doherty et al., 2006) that motivate approach of potentially rewarding cues in the environment (Knutson, Adams, Fong, & Hommer, 2001), as well as to experiencing positive emotions such as excitement (Bjork et al., 2004). Thus, the involvement of this region may account for the overall better rating scores attributed to the hosts who shook hands with guests preceding their social interactions compared with those who did not. Altogether, the behavioral results show that a handshake plays a critical role in creating a favorable impression on a social interaction partner, enhances the effect of approach, and diminishes the negative effect of avoidance social interactions, and the brain imaging findings regarding the role of STS and NAcc provide insight into the neural correlates of these effects. Importantly, given that no significant differences in motion were identified between our conditions, as with previous studies using similar method (Kret, Denollet, et al., 2011; Kret, Pichon, et al., 2011; Pichon et al., 2008, 2009; Peelen & Downing, 2007), we argue that differences in brain activity between different trial types cannot be attributed to differences in the basic amount of motion present in the movies.

Conclusions

Overall, converging evidence provided by our joint assessments of behavioral, brain imaging, and skin conductance data shed light on the role of the social cognition network in evaluating social interaction partners displaying approach and avoidance behaviors. First, approach behavior was associated with more positive evaluations than avoidance behavior, which was reflected in greater ratings for approach than for avoidance and positive covariation of the AMY activity with the behavioral ratings for approach and in negative covariation with skin conductance responses. Second, a handshake preceding social interactions positively influenced the way individuals evaluated the social interaction partners and their interest in further interactions, while reversing the impact of negative impressions. Third, this study provided initial evidence concerning the behavioral and neural basis underlying the positive impact of handshake as a way of formal greeting in social interactions. Collectively, these findings shed light on the neural correlates of evaluating nonverbal social interactions, clarify the role of AMY and STS in evaluating approach and avoidance behaviors, highlight the importance of handshake in creating a favorable impression on social interaction partners, and grant neuroscientific support for the binding power of "[hand]shaking on agreements."

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