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# Neural dissociations between meaningful and mere inconsistency in impression updating

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## Abstract

Recent neuroimaging work has identified a network of regions that work in concert to update impressions of other people, particularly in response to inconsistent behavior. However, the specific functional contributions of these regions to the updating process remain unclear. Using fMRI, we tested whether increases in activity triggered by inconsistent behavior reflect changes in the stored representations of other people in response to behavioral inconsistency, or merely a response to the inconsistency itself. Participants encountered a series of individuals whose behavior either changed in an attributionally meaningful fashion or was merely inconsistent with the immediately preceding behavior. We observed that left ventrolateral prefrontal cortex (vlPFC) and left inferior frontal gyrus (IFG) were preferentially recruited in response to unexpected, immoral behavior, whereas a separate set of regions (including dorsal anterior cingulate cortex, posterior cingulate cortex and temporoparietal junction/inferior parietal lobule) was preferentially recruited in response to more mundane inconsistencies in behavior. These results shed light on the distributed systems supporting impression updating. Specifically, while many regions supporting updating may primarily respond to moment-to-moment changes in behavior, a subset of regions (e.g. vlPFC and IFG) may contribute to updating person representations in response to trait-relevant changes in behavior.

**Key words**: impression updating; impression formation; social cognition; person perception

## Introduction

The ability to form and update impressions of others is a key social faculty, allowing us to predict how others will behave in the future and to tailor our own behavior toward those expectations. However, our understanding of the principles guiding the neural underpinnings of impression updating is in its infancy. Following foundational investigations into the neural bases of behavior-based impression formation (Mitchell *et al.*, 2004, 2005, 2006; Schiller *et al.*, 2009; Cloutier *et al.*, 2011a), subsequent work has taken a more dynamic approach, examining how we change and update impressions over time based upon new information (Harris and Fiske, 2010; Baron *et al.*, 2011; Cloutier *et al.*, 2011b; Kim *et al.*, 2012; Ma *et al.*, 2012; Ames and Fiske, 2013; Bhanji and Beer, 2013; Mende-Siedlecki *et al.*, 2013a,b; Hackel *et al.*, 2015; Stanley, 2015).

Updating is supported neurally by an extended network comprising regions involved in social cognition and impression formation, as well as regions associated with cognitive control and attention (Mende-Siedlecki *et al.*, 2013a). Specifically, medial prefrontal cortex [mPFC, encompassing dorsomedial PFC (dmPFC) and dorsal anterior cingulate (dACC)], lateral prefrontal cortex (lPFC, comprising both rostral and ventral aspects of lPFC), superior temporal sulcus (STS), temporoparietal junction/inferior parietal lobule (TPJ/IPL) and posterior cingulate cortex (PCC) show preferential increases in activity to behavior inconsistent with existing impressions.

Despite strong convergence observed across initial neuroimaging investigations (see Cloutier *et al.*, 2011b; Ma *et al.*, 2012; Mende-Siedlecki *et al.*, 2013b; Hackel *et al.*, 2015), the specific neural contributions supporting impression

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updating remain unclear. Do neural responses triggered by inconsistent behaviors reflect an updated trait representation, or merely surprise at a moment-to-moment discrepancy in behavior? Several regions implicated in updating—dACC, TPJ/IPL and PCC/precuneus—are associated with cognitive processes that might be more strongly linked to the latter account than the former. Meanwhile, other work suggests that a separate subset of regions involved in updating—including ventrolateral prefrontal cortex (vlPFC) and inferior frontal gyrus (IFG)—is recruited by inconsistencies that are diagnostic of an individual's character (Mende-Siedlecki *et al.*, 2013b). We review evidence for these complementary hypotheses below, which, taken together, may reflect a dissociation in the neural bases of updating person impressions.

## Neural responses to mere inconsistencies in behavior

Almost all recent neuroimaging investigations of impression updating have identified the dmPFC as playing a role in updating (Baron *et al.*, 2011; Cloutier *et al.*, 2011b; Ma *et al.*, 2012; Ames and Fiske, 2013; Mende-Siedlecki *et al.*, 2013a, b). For example, Ma *et al.* (2012) observed activity in the dmPFC in response to inconsistent trait inferences, as well as similar activity in more posterior aspects of frontal cortex, including posterior medial frontal cortex (pmFC; e.g. Brodmann area 6) and dACC(e.g. Brodmann area 32), more typically associated with conflict monitoring and control (Ma *et al.*, 2012). Likewise, our initial investigation of updating also observed a large cluster of updating-related activity encompassing the dmPFC, as well as dACC and pmFC (Mende-Siedlecki *et al.*, 2013a). Additional analyses determined that dACC and pmFC were preferentially recruited immediately upon introduction of inconsistent behavioral information, potentially reflecting surprise in response to the inconsistency.

On one hand, the anterior portion of prefrontal cortex typically defined as dmPFC has been well-studied within the social neuroscience literature for its role in social cognition in general, (for review, see Amodio and Frith, 2006; Frith and Frith, 2006; Van Overwalle, 2009), and impression formation in particular (Mitchell *et al.*, 2004; Schiller *et al.*, 2009; Cloutier *et al.*, 2011a; Ferrari et al., forthcoming; Gilron and Gutchess, 2012), so its involvement in updating person representations is not surprising. On the other hand, more posterior regions of the mPFC like the dACC are linked with cognitive processes that are not explicitly social, such as conflict monitoring (e.g. Botvinick *et al.*, 1999, 2004; Kerns *et al.*, 2004), error monitoring (e.g. Carter *et al.*, 1998; Kiehl *et al.*, 2000; van Veen *et al.*, 2004), expectancy violation (e.g. Somerville *et al.*, 2006; Bolling *et al.*, 2011; Hayden *et al.*, 2011) and uncertainty (e.g. Behrens *et al.*, 2008; Cavanagh *et al.*, 2012). Several integrative models have attempted to link these disparate interpretations (e.g. Botvinick, 2007; Alexander and Brown, 2011; Nee *et al.*, 2011; Shenhav *et al.*, 2013). One such account suggests that this region can be understood as an action-outcome predictor (Alexander and Brown, 2011), whose signals reflect 'negative surprise' triggered by actions failing to generate an expected outcome. In this framework, activity in dACC during updating may not reflect an updated representation of a given individual's character, but rather the fact that their behavior is inconsistent with what immediately preceded it.

We note a similar tension arising with regards to parietal areas implicated in previous investigations of updating—IPL and TPJ (Cloutier *et al.*, 2011b; Ma *et al.*, 2012; Bhanji and Beer, 2013; Mende-Siedlecki *et al.*, 2013a,b).

These geographically neighboring but functionally distinct regions are traditionally associated with social cognitive processes that are likely instrumental to the task of impression updating. On the one hand, the IPL is observed to support the perception and understanding of intentional actions (Gallese *et al.*, 2004; Fogassi *et al.*, 2005; Iacoboni *et al.*, 2005; Montgomery and Haxby, 2008), in addition to working memory (McNab *et al.*, 2008; Champod and Petrides, 2010; Van Hecke *et al.*, 2010; Vergauwe *et al.*, 2015). On the other hand, the TPJ is typically associated with theory-of-mind computations regarding the beliefs and motives of others (Saxe and Kanwisher, 2003; Samson *et al.*, 2004; Saxe and Wexler, 2005; Decety and Grèzes, 2006; Völlm *et al.*, 2006; Sommer *et al.*, 2007; Spreng and Grady, 2010; Young *et al.*, 2010a)—though it is not necessarily selective as such (Corbetta and Shulman, 2002; Serences *et al.*, 2005; Corbetta *et al.*, 2008; Mitchell, 2008a; Rothmayr *et al.*, 2011; Chang *et al.*, 2013; Geng and Vossel, 2013).

In the context of social perception, a number of studies have tested direct comparisons that shed light on the functional distinctions between IPL and TPJ. For example, in the same set of participants, IPL was more active during an action-understanding task, whereas TPJ was preferentially engaged by a false belief task (Gobbini *et al.*, 2007). Moreover, in a task designed to dissociate between representations of the implementation of and motives subserving actions, Spunt et al. demonstrated that activity in IPL reflects 'how' processing (i.e. action identification) while activity in TPJ reflects 'why' processing (i.e. attribution of intention based on actions; Spunt *et al.*, 2010, 2011; Spunt and Lieberman, 2012a,b). Finally, during a task where participants attempted to infer the emotional states of targets based on conflicting contextual and non-verbal (i.e. facial expression) cues, activity in TPJ tracked the influence of context, whereas IPL tracked the influence of non-verbal information (Zaki *et al.*, 2010).

Ultimately, while the roles of TPJ and IPL can be functionally dissociated based on the level of abstraction at which they contribute to action understanding and representation, both regions likely support processing the temporary (*vs* dispositional) states of other people (for meta-analysis, see Van Overwalle, 2009). Therefore, recruitment of TPJ/IPL during impression updating may reflect intentionality-related computations tied to specific, unexpected behaviors, as opposed to more global representations of how individuals are generally likely to behave.

Finally, we highlight the PCC/precuneus as another set of regions implicated by previous investigations of updating (Cloutier *et al.*, 2011b; Ma *et al.*, 2012; Mende-Siedlecki *et al.*, 2013a,b) that may be responding to moment-to-moment discrepancies in behavior. While the PCC/precuneus is associated with social cognition, the precise nature of that role is somewhat underspecified (Amodio and Frith, 2006; Mitchell, 2008b; Schilbach et al., 2008; Van Overwalle, 2009; Wolf *et al.*, 2010). The PCC/precuneus is also a key node in the default mode network (Gusnard and Raichle, 2001; Raichle *et al.*, 2001; Greicius *et al.*, 2003; Utevsky *et al.*, 2014), and is implicated in various cognitive processes ranging from autobiographical memory to the representation of subjective value (for review, see Pearson *et al.*, 2011). A recent reconceptualization of the PCC's function suggests that the PCC is responsible for detecting changes in the environment and motivating behavior in order to adapt accordingly (Pearson *et al.*, 2011). In the context of impression updating, PCC/precuneus activity may reflect these changes in behavior, as opposed to the updates themselves.

## This study

We devised a task intended to dissociate neural responses driven by mere moment-to-moment inconsistencies in behavior and neural responses driven by attributionally meaningful inconsistencies. Participants updated their impressions of individuals whose behavior was either inconsistent with respect to a specific, yet quotidian action, or whose behavior was more globally inconsistent within the domain of morality.

We chose to focus on morality because behavior reflecting moral character dominates impression formation, compared with sociability or competence (Wojciszke *et al.*, 1998; Brambilla *et al.*, 2012; Brambilla and Leach, 2014; Goodwin *et al.*, 2014). Moreover, there are clear behavioral predictions regarding what moral behavior is most meaningful: immoral behaviors are more diagnostic than behaviors indicating high moral character (Reeder and Brewer, 1979; Fiske, 1980; Skowronski and Carlston, 1987; Wojciszke *et al.*, 1993; Uhlmann *et al.*, 2015), and trigger larger changes in impressions, both explicitly (e.g. Ybarra, 2001) and implicitly (e.g. Cone and Ferguson, 2014; Mann and Ferguson, 2015). Finally, our previous neuroimaging work suggests that the dominance of immoral behavior in impression updating is evident on a neural level. Activity in left vlPFC and IFG showed preferential increases when participants updated impressions based on immoral behavior (Mende-Siedlecki *et al.*, 2013b; see Supplementary Materials for a replication of this result using data from our initial neuroimaging investigation of updating—Mende-Siedlecki *et al.*, 2013a).

With regards to this study, we predicted (i) that a distributed network of regions observed in previous studies would support updating impressions of both merely and meaningfully inconsistent individuals. Moreover, we predicted that activity in specific components of this network would dissociate as a function of the nature of the inconsistency. While (ii) posterior aspects of PFC (i.e. dACC), TPJ/IPL and PCC should respond preferentially when updating based on 'mere' inconsistencies, (iii) vlPFC and IFG should respond preferentially when updating based on 'meaningful' inconsistencies. Specifically, this latter subset of regions should respond most strongly when updating positive impressions based upon new negative information, compared with updating negative impressions based upon new positive information.

Alternatively, it is possible that regions previously observed to support impression updating are simply responding to expectancy violations in general. The merely inconsistent individuals presented in this study offer the possibility of testing this alternate hypothesis, because the inconsistencies established within these behaviors concern specific actions—they are, in a definitional sense, clearer examples of pure inconsistency. In the absence of a trait concept, 'merely inconsistent' cases might potentially instantiate stronger expectations about a person's future behavior, since identical behaviors should be more predictive of one another than behaviors that are abstractly related, but yet concretely quite different. For example, someone's bedtime on Monday night should predict their bedtime on Tuesday night, more so than 'rescuing a kitten from a tree' should predict 'donating to charity'. That being said, trait concepts do typically guide social learning. As such, we predict that responses in brain regions previously identified to support impression updating in response to diagnostic trait information are unlikely to be explained by such low-level, statistical inconsistencies. Ultimately, this experiment gives a strong test of whether these regions are truly responsive to trait-relevant impression updates as conceptualized in social psychology, as opposed to prediction and expectancy violation as studied elsewhere in cognitive neuroscience.

## Materials and methods

### Participants

Twenty-one (13 female) participants, ages 18–31 ($M = 22.5$, s.d. $= 3.36$), volunteered and received $30 for participation. (This sample size is consistent with our previous investigations of impression updating: $N = 24$, Mende-Siedlecki *et al.*, 2013a; $N = 23$, Mende-Siedlecki *et al.*, 2013b.) Participants were right-handed, had normal or corrected-to-normal vision, and reported no history of neurological illnesses or abnormalities. We acquired informed consent for participation approved by the Institutional Review Board for Human Subjects at Princeton University, and debriefed participants upon completion.

### Face and behavior stimuli

Each participant completed an in-scanner task (adapted from Mende-Siedlecki *et al.*, 2013a,b) in which they learned about the behavior of a series of individuals. Each participant saw 50 male and female faces from the Karolinska Directed Emotional Faces set (Lundqvist *et al.*, 1998), paired with sets of behaviors either previously rated on kindness (Fuhrman *et al.*, 1989) or designed specifically for this paradigm to instantiate an inconsistency regarding a specific, everyday behavior.

Each individual was represented by a male or female face paired with five consecutively viewed behaviors. These sets of behaviors were internally inconsistent in a manner that elicits impression updating. 'Meaningfully inconsistent' individuals were paired with behaviors that reflected moral character. These blocks of trials comprised a face paired with either three positive behaviors, followed by two negative behaviors ('Positive-to-Negative', Figure 1A) or three negative behaviors, followed by two positive behaviors ('Negative-to-Positive', Figure 1B). Positive-to-negative changes were expected to be more diagnostic of an individual's moral character than negative-to-positive changes. For 'merely inconsistent' individuals, information presented on the last two trials again conflicted with information seen during the first three trials, but in a way that was unlikely to trigger an updated representation of the individual's moral character (Figure 1C[1]). As in previous studies, participants also saw control individuals—faces paired with a sentence indicating the individual's name (i.e. 'This man's name is Ron'.)—to control for low-level stimulus attributes (e.g. faces paired with text on screen). In total, participants encountered 50 individuals—20 meaningfully inconsistent (10 Positive-to-Negative, 10 Negative-to-Positive), 20 merely inconsistent and 10 control individuals.

### Procedures

We informed participants that they were participating in a study on impression formation, in which they would see a

1 While we originally intended for "merely inconsistent" sequences of behaviors to focus solely on one specific discrepancy in behavior (i.e., three instances of the same behavior, followed by two instances of a second, inconsistent behavior), behavioral pilot testing suggested that this design might be too monotonous, especially for a scanner task. As such, we introduced a degree of variability in these sequences, such that the second behavior was always a slight variation on the first and third. For example, someone described on Trials 1 and 3 as going to bed at 3 A.M., was described as having a 2:30 A.M. bedtime on Trial 2.

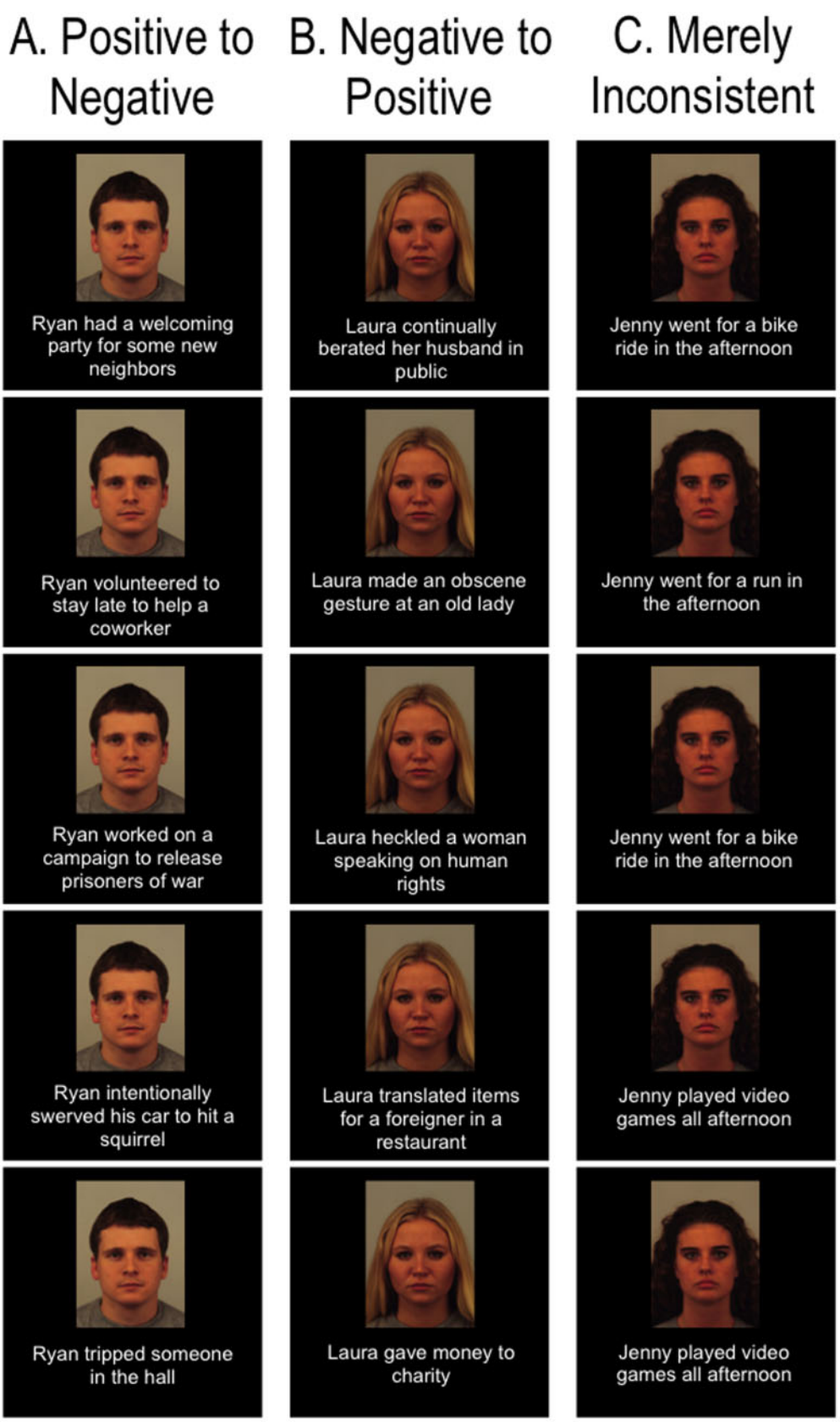


**Fig. 1.** Sample individuals from the positive-to-negative (A), negative-to-positive (B) and merely inconsistent (C) conditions. Faces and behaviors were presented on screen together for 6 s, followed by a 6 s fixation cross. Once all five behaviors were presented, participants provided global ratings of each individual's trustworthiness (4 s) and surprisingness (4 s). KDEF images AM66NES, AF27NES, and AF08NES are from the Karolinska Directed Emotional Faces set, and have been reprinted with the original authors' permission.

series of faces paired with behaviors. Participants were asked to form an impression of each person, and were told that some information might run contrary to the impression they had formed so far. Finally, we told participants that picturing individuals performing behaviors might aid in forming impressions, and that they would make global ratings of trustworthiness and surprise, which should index their overall impression of each individual, taking into account everything they had learned about that person. Participants practiced one run of the task outside the scanner, where they encountered five individuals—comprising faces and behaviors not used in the scanner task.

The scanner task was fundamentally similar to those in our previous neuroimaging investigations of updating, with one critical change. While earlier studies included trial-by-trial ratings following each behavior, this study replaced these trial-by-trial ratings with global ratings of each individual following the final behavior of each sequence. It is possible that trial-by-trial ratings employed in our previous studies (Mende-Siedlecki *et al.*, 2013a,b) may impose an unrealistic demand to continually monitor one's impression of each individual and exaggerate neural activity associated with updating. Therefore, we felt it necessary to assess these evaluations more globally. While it is likely that no ratings need be required for updating to occur, these global ratings (i) facilitated and indexed participants' task engagement and (ii) instilled an explicit impression formation goal in our participants. However, given the global nature of these ratings, they cannot shed light on the magnitude of updates triggered by a given individual's inconsistent behavior. As such, we have chosen not to focus on these behavioral results, though they are reported in Supplementary Materials.

Each individual comprised five consecutive face/behavior pairs. Each single face/behavior pair was presented on screen for 6 s, followed by a fixation cross (6 s). Following the fifth pair, participants rated each individual on trustworthiness (4 s, 'How trustworthy is Sarah?', 4-point scale, 1 = very untrustworthy, 4 = very trustworthy) and surprise (4 s, 'How surprising is Sarah?', 4-point scale, 1 = not at all surprising, 4 = very surprising). (Rating order was counterbalanced between subjects. Half always rated trustworthiness first and half always rated surprise first.) Participants were instructed that when rating surprise, they should take into account how consistent or predictable an individual was. Presentation order was pseudorandomized to ensure that one representative individual of each condition appeared per scanner run.

## Imaging acquisition

Blood oxygenation level-dependent (BOLD) signal was used as a measure of neural activation. Echo planar images were acquired using a Siemens 3.0 Tesla Allegra head-dedicated scanner (Siemens, Erlangen, Germany) with a standard 'bird-cage' head coil at a resolution of $3 \times 3 \times 4$ mm (TR = 2000 ms, TE = 30 ms, flip angle = 80°, matrix size = 64 × 64). By using 32 interleaved 3-mm axial slices we achieved near whole-brain coverage. Prior to the primary data acquisition scans, a high-resolution anatomical image (T1-MPRAGE, TR = 2500 ms, TE = 4.3 ms, flip angle = 8°, matrix size = 256 × 256) was acquired for subsequent registration of functional activity to the participant's anatomy and for spatially normalizing data across participants.

## Imaging analyses

All fMRI data analysis was conducted using Analysis of Functional NeuroImages software (Cox, 1996). The first four EPI images of each run were discarded to allow signal to reach steady-state equilibrium. After slice scan-time correction, participants' motion was corrected using a six-parameter 3D motion-correction algorithm. Transient spikes were removed from the signal using the AFNI program 3dDespike. Subsequently, data were low-pass filtered with a frequency cut-off of 0.1 Hz following spatial smoothing with a 6-mm full-width at half-maximum Gaussian kernel. Anatomical data were then aligned to unsmoothed functional data using the AFNI program align_epi_anat.py, and consequently transformed to Talairach space (Talairach and Tournoux, 1988) using the function @auto_tlrc. Finally, functional datasets were subjected to the same spatial transformation.

To generate parameter estimates, we performed voxel-wise multiple regression on each participant's preprocessed imaging data. Fifteen regressors of interest (5 6000-ms trials per individual × four types of individual: positive-to-negative, negative-to-positive, merely inconsistent and control) were convolved with a canonical hemodynamic response function and entered into our general linear model. Additionally, we included several regressors of no interest, including head motion estimates and time points representing rating slide presentations.

## Whole-brain analyses

First, we identified regions displaying increased activity during the last two (L2) trials, compared with the first three (F3) trials (L2 > F3 contrast), collapsing across all individual conditions (positive-to-negative, negative-to-positive, merely inconsistent and control) in a whole-brain contrast. This contrast identifies regions displaying a main effect of updating.

Moving forward, our primary goal was to identify functional regions of interest where updating activity differed as a function of condition. First, for each participant, we created maps comprising whole-brain activity within F3 and L2 trials, separately, for each of the four individual conditions, resulting in eight maps per participant. These maps were submitted to a 2 (updating: L2 *vs* F3) × 4 (condition: positive-to-negative, negative-to-positive, merely inconsistent, control) ANOVA (whole-brain) using the AFNI command line program 3dANOVA3 to identify brain regions displaying (i) a main effect of updating (e.g. increased activity during L2 trials, compared with F3 trials—L2 > F3), and (ii) more importantly, an interaction between updating and condition. In addition, 3dANOVA3 identified fROIs displaying (iii) a main effect of condition, reported in Supplementary Materials.

Unless otherwise noted, correction for multiple comparisons was performed using the program AlphaSim, which is part of the AFNI package. The Monte Carlo simulation indicated that a minimum cluster extent threshold of 15 voxels was needed to attain a corrected significance of $P<0.05$, at a voxel-wise height threshold of $P<0.001$.

## Extracting parameter estimates from fROIs

3dANOVA3 computes F-statistic maps indicating where activity differs significantly as a function of condition, or the interaction between conditions. To interpret these maps, parameter estimates must be extracted and plotted graphically. Since (i) the main effect of updating is already tested by the L2 > F3 contrast described above—which, as it is a directional test, does not require the extraction of parameter estimates for ease of interpretation—we report the results of the L2 > F3 contrast for parsimony's sake in the results below. However, to interpret

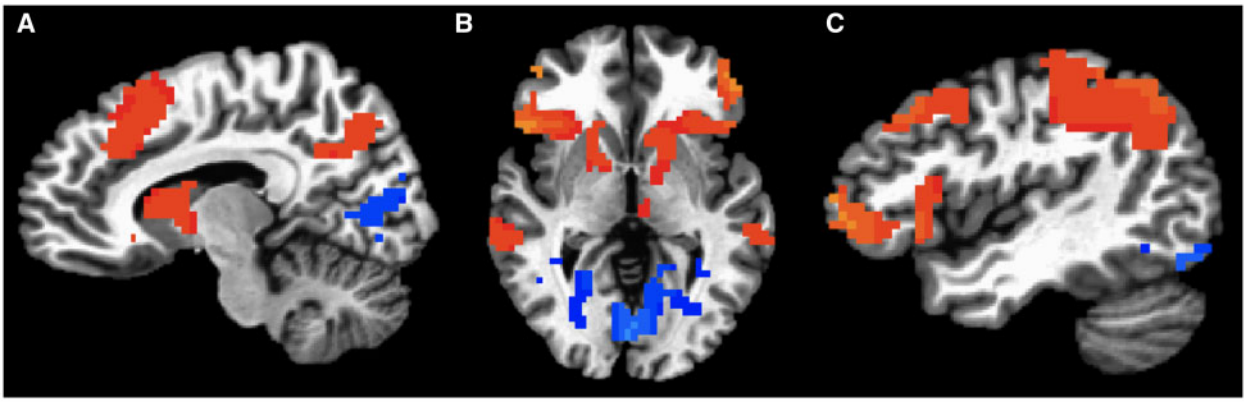


**Fig. 2.** Main effect of updating (last two > first three trials, collapsed across individual type). We observed an extended network of regions that was recruited in response to inconsistent information presented during the last two trials (pictured in hot colors), including (**A**) dmPFC, PCC/precuneus, (**B**) bilateral rlPFC, bilateral vlPFC, bilateral caudate, bilateral STS, (**C**) bilateral ATL and bilateral TPJ/IPL. (Regions pictured in cool colors—including bilateral fusiform gyrus and cuneus—showed preferential responses to information presented on the first three trials, before inconsistent information was introduced). ATL, anterior temporal lobe.

activity within fROIs showing (ii) an interaction between updating and condition [(as well as, iii) a main effect of condition], we extracted and analysed parameter estimates from the F-statistic maps produced by 3dANOVA3, using the AFNI command line program 3dcalc.

### Additional analyses

As a confirmatory step, we performed a series of targeted contrasts aimed at identifying clusters where activity increased from the F3 to L2 trials preferentially for one specific condition. Our primary interests were regions where activity changed preferentially in response to (i) meaningful inconsistencies (e.g. inconsistent negative behavior, compared with inconsistent positive or merely inconsistent behavior) or (ii) mere inconsistencies (e.g. neutral but surprising behavioral information, compared with inconsistent negative or positive behavior). However, we also tested for regions where activity changed preferentially in response to (iii) inconsistent positive behavior, compared with inconsistent negative or merely inconsistent behavior or (iv) either inconsistent negative or positive behavior, compared with mere inconsistency. These data are thresholded as described above: corrected for multiple comparisons ($P<0.05$) with a cluster-extent threshold of 15 voxels (determined by AlphaSim), at a voxel-wise threshold of $P<0.001$.

## Results

### Neuroimaging results

***Main effect of updating.*** We began by performing a whole-brain analysis testing the main effect of updating (L2 > F3, $P$(corrected) < 0.05). This contrast allowed us to isolate regions recruited during updating, independent of condition, and to replicate the results of our previous neuroimaging investigations of updating. We observed a large set of regions that displayed an enhanced BOLD response during L2 trials, compared with F3 trials, including dmPFC, bilateral rostrolateral PFC, bilateral vlPFC extending through IFG, bilateral caudate nucleus, bilateral anterior temporal lobe, bilateral STS, bilateral IPL/TPJ, precuneus and PCC (Supplementary Table S1 and Figure 2). (Regions showing an enhanced BOLD response during F3 trials are also detailed in Supplementary Table S1. See Supplementary Materials and Supplementary Table S2 for information regarding regions displaying a main effect of condition.) Moreover, extensive clusters of activity in occipital and inferotemporal cortex (including bilateral fusiform gyrus) displayed an enhanced BOLD response during F3 trials, compared with L2 trials.

***Interaction between updating and condition.*** Next, we tested for clusters where activity differed as a function of both updating and condition. This contrast allowed us to identify fROIs that might be preferentially recruited by updating impressions based on a specific type of inconsistency (i.e. meaningful *vs* mere inconsistency). We identified 20 such regions (Table 1), extracted parameter estimates from each, and categorized these regions based on the patterns we observed.

Left IFG, left vlPFC and dmPFC (Figure 3A and Table 1A), in addition to three other fROIs, showed preferentially higher activity during L2 trials of positive-to-negative individuals, compared with merely inconsistent or control individuals (which, in turn, showed higher activity compared with negative-to-positive individuals). Additionally, right mid-STS, left posterior STS (extending into TPJ) and pmFC (Figure 3B and Table 1B) showed preferentially higher activity during L2 trials of positive-to-negative, merely inconsistent and control individuals, compared with negative-to-positive individuals.

Furthermore, dACC, mid-ACC and PCC (Figure 3C and Table 1C), in addition to four other regions, showed preferentially higher activity during L2 trials of merely inconsistent and control individuals, compared with either negative-to-positive or positive-to-negative individuals. Finally, four regions (Table 1D) showed preferentially higher activity during L2 trials of control individuals, compared with merely inconsistent individuals (which, in turn, showed higher activity compared with both negative-to-positive or positive-to-negative individuals). See Figure 3 for parameter estimates extracted from key regions identified by the updating-by-condition contrast. For full details on extracted parameter estimates, see the expanded version in Supplementary Figure S1.

***Preferential activity toward updates in response to meaningful inconsistencies.*** Next, we sought to confirm the results of the interaction contrast described above by performing targeted contrasts designed to isolate regions where updating-related

**Table 1.** Regions showing a significant interaction between updating and condition

| Region | Hemi | x | y | z | No. of Voxels |
|---|---|---|---|---|---|
| A. Positive-to-negative > merely inconsistent and control > negative-to-positive. | | | | | |
| IFG | L | −56 | 20 | 18 | 123 |
| vlPFC | L | −47 | 23 | −7 | 37 |
| mFG | L | −41 | −2 | 51 | 56 |
| ATL | L | −41 | 8 | −31 | 25 |
| Anterior temporal pole | L | −53 | 14 | −10 | 21 |
| dmPFC | — | −5 | 59 | 30 | 20 |
| b. Positive-to-negative, negative-to-positive, merely inconsistent > control | | | | | |
| pSTS/TPJ | L | −59 | −53 | 12 | 331 |
| Mid-STS | R | 65 | −41 | 3 | 64 |
| Posterior medial frontal cortex | — | −2 | −2 | 66 | 58 |
| C. Merely inconsistent and control > positive-to-negative and negative-to-positive | | | | | |
| dACC | — | 2 | 23 | 30 | 85 |
| Mid-ACC | — | −2 | 2 | 42 | 80 |
| Superior frontal gyrus | L | −35 | 44 | 30 | 34 |
| ATL | L | −56 | 5 | −1 | 32 |
| PCC | — | 5 | −38 | 48 | 29 |
| Mid-ACC | — | 2 | 11 | 39 | 23 |
| Cerebellum | R | 17 | −35 | −40 | 19 |
| D. Control > merely inconsistent > positive-to-negative and negative-to-positive | | | | | |
| Calcarine sulcus/cerebellum | — | −5 | −56 | 9 | 1119 |
| mPFC | — | 2 | 56 | 12 | 39 |
| Parahippocampal gyus | R | 29 | −26 | −22 | 26 |
| Mid-STS | R | 65 | −20 | 12 | 17 |

ATL, anterior temporal lobe. Group results ($N = 21$), corrected for multiple comparisons at a voxel-wise threshold of $P<0.001$ and a cluster-extent threshold of 15 voxels (determined by AFNI's AlphaSim package). Coordinates refer to the peak voxel in Talairach space, and are rounded to the nearest integer. For each cluster, we report its hemisphere (Hemi) and size in voxels (no. of voxels). Note: Rather than referring to specific contrasts run, Table 1 sub-headings are meant to be descriptive of the general patterns of parameter estimates extracted from each region displaying an interaction between updating and condition.

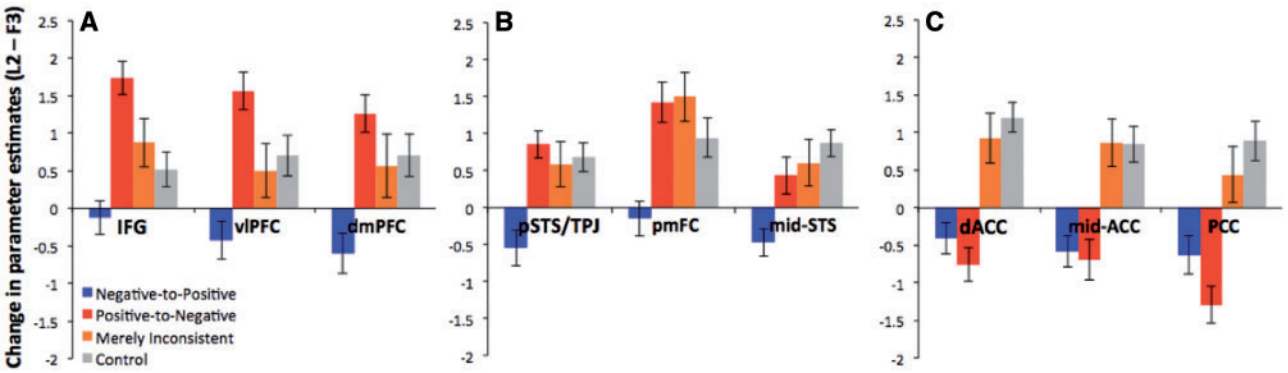


**Fig. 3.** Parameter estimates extracted from regions displaying an interaction between updating and condition. Colored bars indicate the change in activity from the first three to the last two (i.e. update-provoking) trials. Here, we provide information on selected key regions emerging from the updating-by-condition interaction in which (**A**) the updating-related change in activity was strongest for positive-to-negative individuals, (**B**) this change in activity was stronger for positive-to-negative, merely inconsistent and control individuals, compared with negative-to-positive individuals, and (**C**) this change in activity was stronger for merely inconsistent and control individuals, compared with individuals from either meaningfully inconsistent condition. (Blue = negative-to-positive, red = positive-to-negative, orange = merely inconsistent, gray = control.) Error bars indicate ±1 standard error. (For an expanded version of this figure including all 20 regions identified by the updating-by-condition interaction contrast, see Supplementary Figure S1.).

activity was especially strong in response to one particular kind of inconsistency.

First, we tested for regions showing a preferential increase in activity when updating based on inconsistent negative behavioral information, compared with inconsistent positive, merely inconsistent or control trials. A whole-brain contrast revealed that left IFG and left vlPFC, as well as left middle frontal gyrus all displayed a bias toward updating based on immoral behaviors (Table 2A and Figure 4A).

***Preferential activity toward updates in response to mere inconsistencies.*** Next, we tested for regions showing a preferential increase in activity when updating based on mere inconsistencies, compared with inconsistent positive or negative behaviors, or control trials (Table 2B and Figure 4B and C). A whole-brain contrast revealed twelve regions displaying a pattern of mere inconsistency-specific activity, including dACC, mid-ACC and PCC/precuneus, as well as bilateral TPJ/IPL.

**Table 2.** Regions showing dissociation between updating based on meaningful information and a response to mere inconsistency

| Region | Hemi | x | y | z | No. of voxels |
|---|---|---|---|---|---|
| A. $L2>F3_{Positive\text{-}to\text{-}negative} > L2>F3_{Negative\text{-}to\text{-}positive}$, $L2>F3_{Mere\ inconsistency}$ and $L2>F3_{Control}$ | | | | | |
| IFG | L | −56 | 20 | 18 | 98 |
| vlPFC | L | −50 | 26 | −−4 | 47 |
| mFG | L | −41 | −2 | 51 | 19 |
| B. $L2>F3_{Mere\ inconsistency} > L2>F3_{Positive\text{-}to\text{-}negative}$, $L2>F3_{Negative\text{-}to\text{-}positive}$ and $L2>F3_{Control}$ | | | | | |
| TPJ/IPL | R | 44 | −50 | 48 | 66 |
| TPJ/supramarginal gyrus | L | −44 | −32 | 36 | 45 |
| PCC | — | 2 | −29 | 30 | 31 |
| dlPFC | L | −35 | 26 | 36 | 30 |
| Superior frontal gyrus | R | 26 | 8 | 57 | 28 |
| Precuneus | R | 14 | −50 | 42 | 22 |
| Precuneus | R | 11 | −72 | 39 | 21 |
| dACC | — | 2 | 23 | 30 | 16 |
| TPJ/IPL | L | −47 | −53 | 39 | 16 |
| Mid-ACC | — | 2 | 11 | 39 | 16 |

mFG, middle frontal gyrus. Group results ($N = 21$), corrected for multiple comparisons at a voxel-wise threshold of $P<0.001$ and a cluster-extent threshold of 15 voxels (determined by AFNI's AlphaSim package). Coordinates refer to the peak voxel in Talairach space, and are rounded to the nearest integer. For each cluster, we report its hemisphere (Hemi) and size in voxels (no. of voxels).

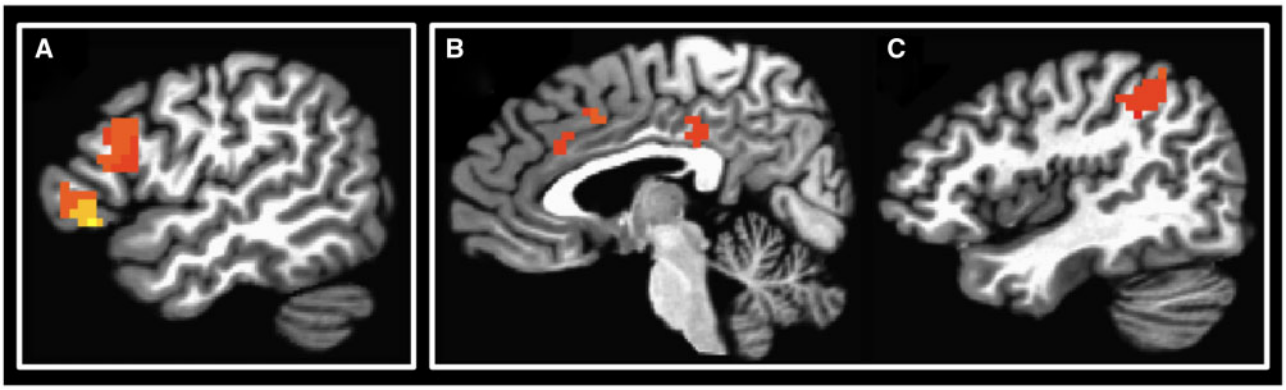


**Fig. 4.** Preferential neural responses to meaningful and mere inconsistency. Left vlPFC and left IFG (Panel A), showed enhanced activity when updating based on immoral behaviors, compared with updates based on moral or merely inconsistent behaviors. dACC, mid-ACC, PCC (Panel B), and right TPJ/IPL (Panel C) all showed enhanced activity when updating based on merely inconsistent behaviors, compared with updates based on moral or immoral behaviors.

***Additional contrasts.*** Finally, we tested whether any regions showed a preferential response to (i) updating based on inconsistent positive behavioral information, compared with negative, merely inconsistent and control trials, or (ii) updating based on either positive or negative behaviors, compared with merely inconsistent behaviors or control trials. Neither contrast revealed any significant clusters of activity.

## Discussion

Our results suggest a dissociation between brain regions supporting behavior-based impression updating. While several regions (e.g. left vlPFC and IFG) displayed enhanced responses to meaningful, negative information particularly diagnostic of moral character, an additional subset of regions (e.g. dACC, TPJ/IPL, PCC) responded preferentially to inconsistencies of a more immediate, yet mundane nature.

Multiple analyses suggested that left vlPFC and left IFG displayed preferentially stronger activity when updating initially positive impressions of moral character with new negative information, relative to negative-to-positive updates, updates based on mere inconsistency or control trials. This negativity bias during updating based on moral behavior is consistent with previous literature (Reeder and Spores, 1983; Reeder and Coovert, 1986; Skowronski and Carlston, 1987; Wojciszke *et al.*, 1993; Wojciszke, 2005). These results also dovetail with our own neuroimaging investigations of updating. First, while our initial study did not test for interactions between valence and updating (Mende-Siedlecki *et al.*, 2013a), re-analysis of these data confirms left vlPFC and left IFG showed preferential responses when updating based on immoral behaviors, compared with moral behaviors (Supplementary Materials, Figure S2 and Table S3). Moreover, a subsequent investigation comparing updating based on moral behaviors *vs* behaviors related to ability (Mende-Siedlecki *et al.*, 2013b) determined that bilateral vlPFC and left IFG (as well as left STS) responded preferentially to diagnostic information from either domain (e.g. immoral behaviors and competent behaviors).

This previous study suggested that rather than displaying a pervasive negativity bias during updating, the brain is particularly responsive to behaviors that are perceived to be statistically infrequent in the environment—negative behaviors in the morality domain and positive behaviors in the ability domain. The diagnosticity of a given behavior, and thus its

meaningfulness, is an emergent property of perceived frequency: less common behaviors have a stronger impact on our impressions of others. We interpret the present data through this lens, as negative, immoral behaviors are robustly perceived to occur with less frequency than their positive counterparts (Kanouse and Hanson, 1972; Rothbart and Park, 1986; Funder and Dobroth, 1987; Tausch *et al.*, 2007; Mende-Siedlecki *et al.*, 2013b). In a sense, echoing the work of Harold Kelley (Kelley, 1967, 1973), one key determinant of what makes a behavior attributionally meaningful is its distinctiveness. Immoral behavior provides more informational value about the true character of an individual (Uhlmann *et al.*, 2015), and likely offers more predictive capability regarding their future behavior.

One interesting implication of the frequency account is that diagnosticity should be sensitive to context, varying from environment to environment. In an environment where deceptive, anti-social, or criminal behavior is common, learning that someone has behaved immorally may carry less informational value (e.g. Barclay, 2008; Peysakhovich and Rand, 2016). In such environments, positive, moral behaviors may be perceived as less frequent, and might therefore lead to stronger impression updates. By the same token, this logic extends to the sorts of behaviors employed by our 'merely inconsistent' condition. In a context in which these behaviors are perceived to be particularly rare, or with a task framing that makes them more meaningful (e.g. learning about preferences), we might expect similar neural patterns of updating-related responses.

However, we do not mean to suggest that the contributions of the vlPFC and IFG to impression updating are 'specifically social' in nature. Indeed, vlPFC and IFG have been extensively implicated in domain-general cognitive processes related to working memory and interference resolution (Thompson-Schill *et al.*, 2002, 2005; Kan and Thompson-Schill, 2004; Jonides and Nee, 2006). Additional work has clarified the contributions of these regions, distinguishing between the role of the anterior vlPFC (or IFG *pars orbitalis*, corresponding to the left vlPFC cluster observed in this study) in the controlled, top-down retrieval of stored conceptual representations, and the role of the more posterior mid-vlPFC (IFG *pars triangularis*, corresponding to the left IFG cluster observed in this study) in resolving competition between retrieved representations (Badre and Wagner, 2005, 2007; Souza *et al.*, 2009; Satpute *et al.*, 2014). Moreover, this region has been implicated in a process paralleling those isolated in the present task, yet without any social context—encoding changing representations of objects over time (Hindy *et al.*, 2012, 2015). Ultimately, while we have observed evidence across three datasets that vlPFC and IFG support updating person impressions based upon attributionally meaningful information, we would suggest that this represents an instance of a domain-general mechanism being recruited in service of a social process.

In contrast to the regions responding to attributionally meaningful behavioral information during updating, a separate subset of regions responded preferentially to mere inconsistencies in behavior. These included several clusters within the cingulate cortex (dACC, mid-ACC, PCC), as well as clusters in lateral parietal cortex comprising aspects of TPJ and IPL.[2] Moreover, we note that in general, these regions were less responsive to updates based on attributionally meaningful changes in behavior (though see Footnote 2). Taken together, these results suggest that in the context of updating person representations, these regions are particularly sensitive to changes in behavior that reflect more short-term states or intentions, as opposed to more dispositional, trait-level inconsistences, consistent with prevailing interpretations of the functions of these regions (e.g. outcome-specific surprise in dACC, Alexander and Brown, 2011; theory-of-mind computations in TPJ, Van Overwalle, 2009).

One might argue that a limitation of this investigation stems from potential differences in arousal across the different types of individuals participants learned about in the updating task. Indeed, while individuals in the merely inconsistent condition were rated as being significantly more surprising than the control condition, they were also rated as being less surprising than either the positive-to-negative or negative-to-positive conditions (Supplementary Materials). If it were simply the case that no regions responded to the mere inconsistencies presented in this task, an arousal explanation might be more compelling. However, we observed a number of such regions (e.g. dACC, TPJ/IPL, PCC), which we predicted would track specific, moment-to-moment changes in behavior based on previous accounts of their function (see **Introduction**). Moreover, for the difference in surprise ratings to explain the neural differences between responses to mere and meaningful inconsistency, there should also be a difference in surprise ratings between positive-to-negative and negative-to-positive individuals. Indeed, despite the differences in updating-related activity between positive-to-negative and negative-to-positive individuals, both types of individuals were rated as similarly surprising (Supplementary Materials).

Regardless, we note that using global ratings did not produce divergent neuroimaging results compared with previous studies employing trial-by-trial ratings. This convergence suggests trial-by-trial ratings did not artificially inflate our previous imaging results by imposing an unnatural demand to update, and gives additional confidence in the results of our prior work (Mende-Siedlecki *et al.*, 2013a,b).

## Conclusions

Ultimately, these data offer an answer to the question posed at the outset—whether activity in regions involved in impression updating reflects an updated trait representation of a given individual, or merely a response to an immediate discrepancy in behavior. The results demonstrate that when learning new information about other people, a subset of regions involved in updating impressions (left vlPFC and IFG) responds preferentially to attributionally meaningful information—particularly behaviors indicative of low moral character. However, a separate subset of regions (dACC, IPL/TPJ, PCC) responds more strongly to more mundane, moment-to-moment inconsistencies in behavior. While this study marks a positive first step in understanding the different yet complementary roles of regions involved impression updating, further work should continue to pursue more fine-grained specifications of the computational contributions of these regions.

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2 Though the targeted contrast yielded clusters in bilateral TPJ/IPL responding preferentially to merely inconsistent individuals, the updating-by-condition interaction did not produce activations in this vicinity. However, the interaction contrast identified a larger cluster comprising both left STS and TPJ, where updating-related activity did not differ between the positive-to-negative, negative-to-positive, and merely inconsistent conditions.

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## Supplementary data

Supplementary data are available at *SCAN* online.

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