

Perceptual Observer Modeling Reveals Likely Mechanisms of Face Expression Recognition Deficits in Depression

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ABSTRACT

BACKGROUND: Deficits in face emotion recognition are well documented in depression, but the underlying mechanisms are poorly understood. Psychophysical observer models provide a way to precisely characterize such mechanisms. Using model-based analyses, we tested 2 hypotheses about how depression may reduce sensitivity to detect face emotion: 1) via a change in selectivity for visual information diagnostic of emotion or 2) via a change in signal-to-noise ratio in the system performing emotion detection.

METHODS: Sixty adults, one half meeting criteria for major depressive disorder and the other half healthy control participants, identified sadness and happiness in noisy face stimuli, and their responses were used to estimate templates encoding the visual information used for emotion identification. We analyzed these templates using traditional and model-based analyses; in the latter, the match between templates and stimuli, representing sensory evidence for the information encoded in the template, was compared against behavioral data.

RESULTS: Estimated happiness templates produced sensory evidence that was less strongly correlated with response times in participants with depression than in control participants, suggesting that depression was associated with a reduced signal-to-noise ratio in the detection of happiness. The opposite results were found for the detection of sadness. We found little evidence that depression was accompanied by changes in selectivity (i.e., information used to detect emotion), but depression was associated with a stronger influence of face identity on selectivity.

CONCLUSIONS: Depression is more strongly associated with changes in signal-to-noise ratio during emotion recognition, suggesting that deficits in emotion detection are driven primarily by deprecated signal quality rather than suboptimal sampling of information used to detect emotion.

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Understanding the mechanisms that underlie diseases, which for mental disorders correspond to pathological modes of information processing, is a goal in psychiatry. Computational modeling provides tools to formalize the mechanisms that underlie typical information processing and to precisely characterize how those mechanisms are influenced by disease, which leads to observable abnormal behavior (1–3).

Multiple psychiatric disorders (4–10) are accompanied by changes in perception of face emotion. More specifically, depression is associated with a general impairment in the processing of emotional faces and a tendency to interpret ambiguous faces (e.g., neutral or morphed) as expressing negative emotion (11–14). The latter bias, as well as deficits in the recognition of happiness but not sadness (13–15), is explained best by a lower sensitivity toward happiness (and other emotions) rather than by a higher sensitivity toward negative emotion (15). However, it is not clear exactly what mechanism leads to such reduced sensitivity.

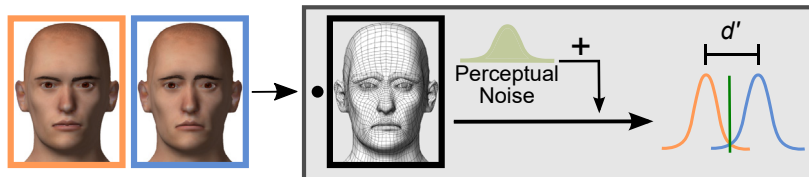
Observer models from psychophysics (16) provide a way to precisely characterize changes in the detection of face

expressions. The simplest of these models, the linear observer model (LOM) (17–20) depicted in Figure 1A, assumes that the visual system stores a template that summarizes the expected properties of a stimulus that contains a particular expression. An incoming stimulus is compared against this template to determine evidence for the presence of the target expression, which in turn is distorted by internal noise. The resulting sensory evidence variable is compared against a threshold to determine whether the system would classify the stimulus as containing or not containing the expression.

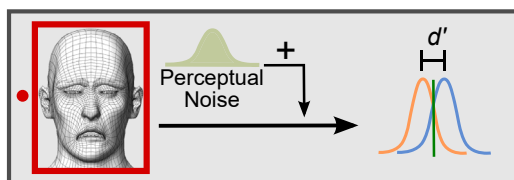
Two mechanisms can explain a reduction in sensitivity to detect a target expression. First, depression may produce a change in the face information used to detect expression (Figure 1B) or the channel's selectivity. Trouble recognizing expressions would result from suboptimal information sampling compared to typical functioning. Second, depression may produce an increase in the channel's noise or, correspondingly, a scaling down of the sensory evidence signal, i.e., a reduction in signal-to-noise ratio.

SEE COMMENTARY ON PAGE 549

A Linear Observer Model



B Change in Channel Selectivity



C Change in Signal-to-Noise Ratio

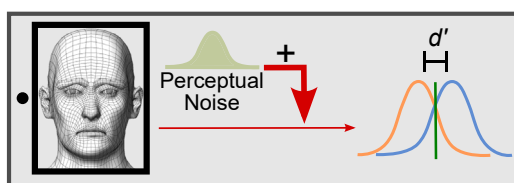


Figure 1. (A) The linear observer model and 2 mechanisms through which depression could reduce the sensitivity (d') to detect emotion in a face: (B) by changing the face information used for emotion detection or (C) by changing the signal-to-noise ratio in the system in charge of detection.

Reverse correlation is a technique used to estimate the LOM template depicted in Figure 1A. Across many trials, participants are presented with noisy stimuli, and their choices about the presence or absence of the target expression are recorded. Regressing choices on the presented noise patterns produces weights that are proportional to the observer’s template. While related techniques have been applied in psychiatric research (21–23), no previous study has used the LOM to determine the mechanisms implied by an estimated template. Observer models are generative (3), which means that they can be presented with stimuli to generate choice data and underlying variables, which can then be compared with experimental data. Such model-based analyses could offer important insights into the mechanisms of perceptual dysfunction.

Here, we used the framework depicted in Figure 1 to determine whether the changes in face expression perception observed in depression could be explained better by changes in the information used to detect expression (i.e., the selectivity hypothesis) or by a reduction in the signal-to-noise ratio during detection of an expression (i.e., the signal-to-noise hypothesis). Sixty adults, one half fitting criteria for major depression disorder (MDD) and the other half healthy control participants, completed 2 sessions of a reverse correlation task. They were asked to identify sadness and happiness in noisy face stimuli, and their responses were used to estimate templates used for emotion identification. We analyzed these templates using traditional analyses and model-based analyses, in which templates were matched against stimuli to obtain sensory evidence variables that we compared against behavioral data.

METHODS AND MATERIALS

Participants

Sixty adult participants from the Austin, Texas, area were recruited for this study, half of them ($n = 30$) in the MDD

group and the other half ($n = 30$) in the control group (for recruitment procedures and inclusion/exclusion criteria, see the Supplement). All participants were screened using the Quick Inventory of Depressive Symptomatology–Self-Report (24) and the Mini-International Neuropsychiatric Interview (25). Demographic and clinical information about the study participants is presented in Table 1.

Participants in the MDD group were screened to have a score of 11 or higher on the Quick Inventory of Depressive

Table 1. Demographic and Clinical Characteristics of the Sample

	Major Depressive Disorder	Control
Age, Mean [Range]	21.49 [18–34]	23 [19–35]
Sex, Female, %	70%	73%
Race and Ethnicity, %		
African American or Black	13%	17%
American Indian or Alaska Native	3%	10%
Asian	30%	23%
Hispanic-Latino	23%	33%
White	43%	47%
More than one race or none applicable	13%	7%
QIDS-SR Score, Mean [Range]	15.23 [11–22]	2.43 [0–4]
Past Episode of Depression, %	90%	0%
First Episode of Depression, %	10%	0%
Age at First Onset of Depression, Mean (SD)	16.33 (4.05)	–
Number of Episodes of Depression, Mean [Range]	6.04 [2–27]	–

There were no significant differences between groups on any of the demographic variables reported (all $ps > .1$).

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Symptomatology–Self-Report and to meet DSM-5 criteria for MDD according to the Mini-International Neuropsychiatric Interview. Participants were excluded if they had current or past bipolar disorder, psychotic disorder, and/or schizophrenia. Participants in the control group were excluded if they had any current or past psychiatric disorder. They were screened to have a score of 6 or less on the Quick Inventory of Depressive Symptomatology and to never have experienced an episode of MDD. As shown in Table 1, the average participant with MDD was experiencing depression of moderate severity, whereas every control participant was experiencing little to no depression. We did not assess history of medication use.

Participation was voluntary, and participants were compensated at a rate of \$20/hour. All procedures were approved by the Institutional Review Board of the University of

Texas at Austin, and written informed consent was obtained from all participants by study personnel prior to the start of the experiment.

Stimuli

All stimuli presented in the main task consisted of pixel luminance noise superimposed on a base face image (Figure 2B). The base images were high-resolution grayscale renderings from previously validated 3-dimensional models of 3 identities (26), each showing a neutral expression, which permits strong stimulus control for any facial feature that is of no interest. The 3 models were 2 specific identities (“Bob” and “Joe”) plus the average of 24 identities, half male and half female. The same skin texture was used in all models. A different noise pattern

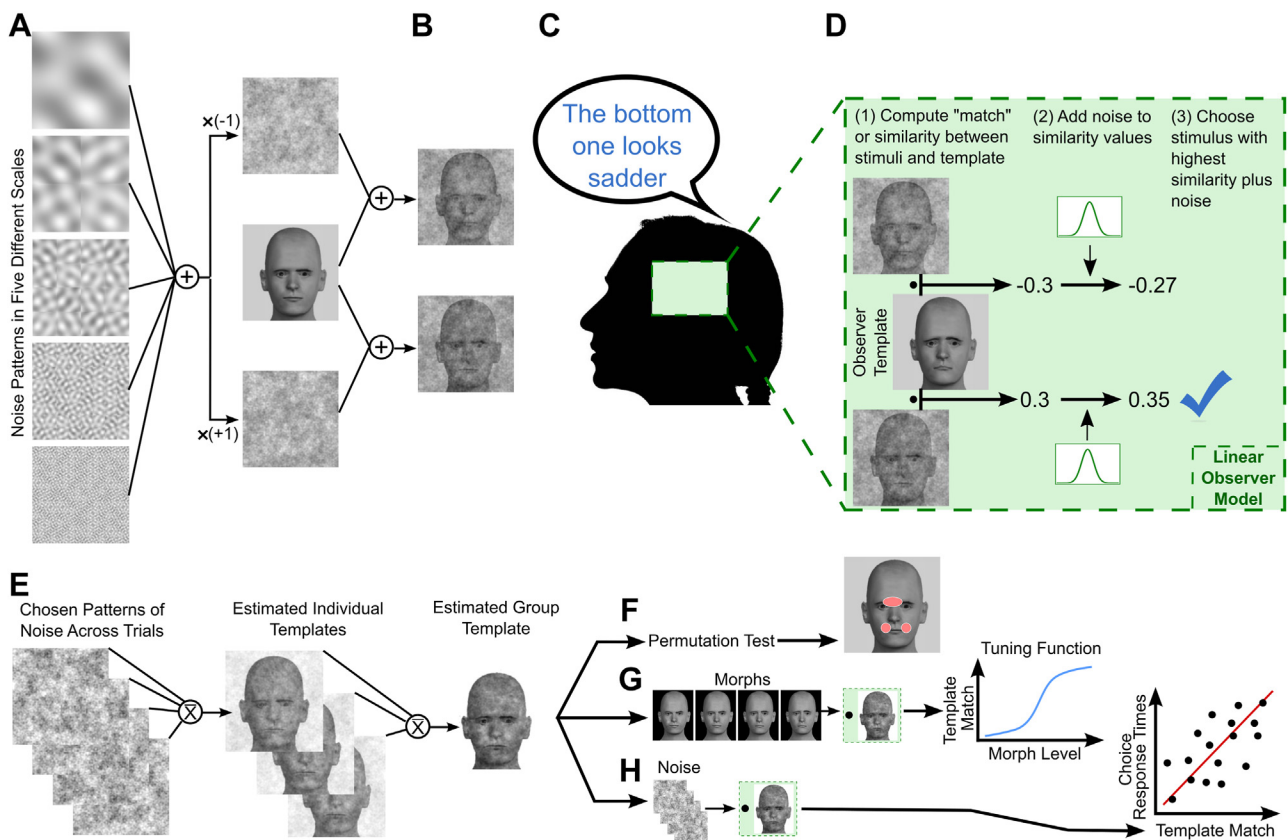


Figure 2. Summary of methodology used in this study. **(A)** On each trial, stimuli were created by sampling noise patterns in 5 different scales (i.e., sizes) and adding them together. The resulting summed noise pattern was multiplied by +1 and -1 and superimposed on a base image with a neutral expression, resulting in **(B)** 2 noisy stimuli presented to the participant, in which the patterns of lightness and darkness were opposite due to the 2 opposite noise patterns. **(C)** Participants were asked to choose which of the 2 stimuli looked more like a target emotion (sad or happy). **(D)** According to the linear observer model (LOM), the 2 stimuli are matched against an internal template, resulting in a variable that represents the level of sensory evidence for the template in the stimuli. Perceptual internal noise disrupts the process. The observer chooses the stimulus with the highest match or similarity with the template. **(E)** To estimate the internal template, we averaged all the chosen patterns of noise across trials, which yielded 1 estimate per participant. These were then averaged to obtain a single estimate for each group (major depressive disorder and control). **(F)** A permutation test was used to determine areas in the estimated group templates that were used significantly by each group and differently between groups. Red blobs illustrate significant face areas in the permutation test. **(G)** A series of faces morphed from a target identity to its anti-identity (going through neutral) was matched against the estimated group templates, which corresponds to the first step of processing in the LOM. The result was a tuning function showing the level of match or average model response as a function of morph level. **(H)** The noise presented to each participant during each trial was matched against the estimated group templates, corresponding to the first step of processing in the LOM. The resulting values were correlated with response times, which we assume are a reflection of sensory evidence (i.e., higher evidence leading to faster response times). A lower signal-to-noise ratio in the LOM (e.g., due to increased perceptual noise) should produce a reduction in this correlation.

was created for each trial using a weighted sum of sinusoids (Figure 2A) as proposed in Mangini and Biederman (27). Adding and subtracting the noise pattern from the base image produced 2 stimuli per trial. For a more detailed explanation of how base stimuli and noise masks were created, see the Supplement.

Procedure

In 2 different sessions of 90 minutes each, we asked participants to detect happiness and sadness in noisy face stimuli (Figure 2C).

Each session started with a familiarization task. Participants were instructed that their first task would be to learn the faces of 2 unfamiliar people. Then, they were presented with 2 videos (60 seconds), each showing a different face through changes in camera viewpoint and emotional expression. Each video was repeated twice and was accompanied by the name of the face that was presented (Bob or Joe) and instructions to memorize the face. This was followed by the main task.

During the happiness detection session, participants were asked to identify which of 2 noisy stimuli (presented side by side) looked happier. Three different base identities were used in different blocks of 100 trials. There were 5 blocks with each base identity, for a total of 500 trials per identity and 1500 total. The session was created by cycling through the 3 block types, presented 5 times in random order. This design allowed us to determine both the information used to identify happiness across identities and whether changing identities had any influence over that information.

Identical procedures were used in the sadness detection session, but with participants being asked to identify which of the 2 noisy stimuli looked sadder. Participants participated in an additional session focused on face identification, which we do not report on here.

The task and stimuli used in this study are available online at https://osf.io/4amuw/?view_only=7e5caedbea2b4615ba43a6a476b21e8d.

Classification Image Analysis

The goal of these analyses was to determine whether any differences could be found between groups in the information used for detection of face emotion. As such, these analyses can only provide information regarding the selectivity hypothesis.

For each participant and base identity, we estimated a template by averaging selected noise patterns through the R package *rcicr* (28) and selecting only pixels inside the face by using an oval mask. The final templates are grayscale images with a single intensity value at each pixel. We obtained average templates for each group, both across all identities and for each specific identity (Figure 2E).

Dissimilarity Analysis. We measured the dissimilarity between the average templates of the 2 groups using $d = (1 - r)/2$, where r is the Pearson correlation coefficient. This measure ranges from 0 (perfectly similar) to 1 (perfectly dissimilar). Note that d reveals differences in the spatial distribution of areas used for recognition, while discarding information about the magnitude of such differences (i.e., dissimilarity in the pattern

of dark and light pixels leading to emotion detection, regardless of their specific magnitude) because reverse correlation produces estimates that are only proportional to the true templates. We performed a permutation test to determine the significance of d . In this test, the labels of the 2 groups were randomly shuffled, followed by template averaging and computation of d . The empirical distribution of d across 5000 repetitions was used to compute a p value for the test.

Local Cluster Analysis. To determine in a bottom-up manner whether the 2 groups used information differently within any local face area (i.e., a cluster of adjacent pixels with similarly lighter or darker luminance in the estimated template), we subtracted the MDD template from the control template to obtain a difference template. We used threshold-free cluster enhancement (29) to amplify any local signals of differences between groups. Then, we performed a permutation test (shuffling group assignment) to determine whether any difference signals were significant (Figure 2F). We performed an additional permutation test (shuffling the sign of signals across participants) to determine which local areas of the face were used by each group to identify happiness and sadness. Both permutation tests used 2000 iterations to build empirical distributions for p value estimation. For a more detailed description of this analysis, see the Supplement.

Model-Based Analysis

To test the selectivity and signal-to-noise hypotheses more directly, we turned to model-based analyses in which we used the estimated templates to determine how the LOM (Figure 2D) would respond to face stimuli directly presented to it. We pooled data across identity blocks and participants to obtain more accurate estimates of the happiness and sadness templates of each group that are adequate for model-based analyses. As mentioned earlier, the LOM proposes that happiness and sadness identification are achieved by matching the information in an incoming image and the corresponding template, using a dot product operation. The output value represents the evidence that the input image contains the target signal.

Selectivity Analysis. We presented the model with the average identity (see Stimuli) varying in expression from a target expression to neutral, and then to its antiexpression, in 30 morphing steps (Figure 2G). We obtained morphed continua for both happiness and sadness expressions [using the validated expression models from (27)] and presented those stimuli to the corresponding estimated LOM, which resulted in curves showing the model's output as a function of expression intensity. Each curve was rescaled to have a minimum value of 0. These tuning curves represent the selectivity of the model to expression intensity, and thus they should increase with expression intensity. Thus, differences in tuning curves represent differences in selectivity. We used a nonparametric bootstrap procedure (2000 iterations; resampling participants' templates before averaging) to obtain 84% confidence intervals for these curves, where no overlap corresponds to a 2-sample significance test with $\alpha = 0.05$ (30).

Signal-to-Noise Analysis. We presented the noise shown to participants as input to the model, and its outputs were recorded (Figure 2H). The model's output was determined exclusively by the match between patterns of noise and the template (i.e., no internal source of noise was added, see Figure 1A). However, people's behavior depends not only on the match between noise patterns and a constant template but also on added internal noise; the higher this noise is, the lower the correlation should be between the model's predictions and people's choice behavior. We used recorded response times because they are independent from the data used to estimate the templates, but in theory they should be related to sensory evidence. For each participant, we computed the Pearson correlation between the absolute value of the model's output and the response time across experimental trials. These correlations should be negative because stronger perceptual evidence should produce smaller (i.e., faster) response times. If depression is accompanied by higher internal noise in the perception of expression, then these correlations should be closer to 0 and significantly different from those observed in healthy control participants. We used a Welch 2-sample *t* test to test for differences between groups in this analysis.

Template Invariance Analysis

Finally, we asked whether depression could influence the invariance of representations of emotion to changes in identity. This question is important because face expression processing can be highly context specific (31), and depression could reduce or increase the degree to which identity information is integrated into perceived expression during face processing. We tested the invariance of templates by estimating separate templates for each of the 3 different identities included in the study and measuring their similarity via Pearson correlation (32). These correlations were input into a 3 (identity pair) \times 2 (group) analysis of variance.

For more details on procedures and session timing, see the Supplement.

RESULTS

Information Used for Face Expression Recognition Was Mostly Preserved in Depression

The obtained templates are shown in Figure 3. The templates estimated using all 1500 trials in the experiment are highlighted inside the gray box, whereas templates obtained from specific base identities are to the right of that box. The templates were similar between groups with the exception of the templates for sadness at the average identity.

The dissimilarity between the templates obtained from the 2 groups was not significantly different from chance in the analysis of happiness ($d = 0.38$, $r = 0.24$, $p = .30$) or sadness ($d = 0.45$, $r = 0.10$, $p = .55$). In additional analyses, the same results were found for individual identities.

Figure 3 shows the significant areas from the cluster analysis, with areas significantly used by the control group in blue, areas significantly used by the MDD group in red, and significant differences in green. Analyses without any significant tests are represented by black silhouettes. Areas that were significantly used by both groups in the detection of happiness

were limited to the area next to the oral commissures, where darker pixels produced the impression of a smile. No significant differences were found between groups. In the analysis of sadness, most of the information observable in the templates shown in Figure 3 was not significant. The exception was the template obtained at the average identity for the MDD group, which showed a significant darkening of the left eyebrow. Because the control group's template did not show the same feature, their difference was also significant around the same area.

The permutation tests used in these analyses can be conservative. To increase statistical power, we repeated the analyses focused on areas around the eyes and mouth. Despite the reduction in the number of pixels included (which should increase power), the results were similar, and the conclusions did not change.

Depression Was Associated With Reduced Signal-to-Noise Ratio in the Detection of Happiness

The results of the model-based analyses are presented in Figure 4. In Figure 4A, results of the selectivity analysis show that tuning curves increased with expression intensity, with the MDD group showing a weaker response to changes in happiness and a stronger response to changes in sadness. Nevertheless, overlapping confidence intervals indicate that the differences were nonsignificant.

In Figure 4B, results of the signal-to-noise analysis show a different picture. For happiness, the mean correlation between the model's predicted output and response times was significant in the control group ($t_{29} = -3.25$, $p = .006$, Cohen's $d = -0.6$) but not in the MDD group ($t_{29} = 0.33$, $p = .747$, Cohen's $d = 0.06$), and the difference between groups was significant ($t_{52.08} = 2.14$, $p = .037$, Cohen's $d = 0.59$). This suggests a weaker signal-to-noise ratio during happiness detection in depression. For sadness, the mean correlation between the model's predicted output and response times was not significant in either the control group ($t_{29} = 1.53$, $p = .137$, Cohen's $d = 0.28$) or the MDD group ($t_{29} = -1.65$, $p = .110$, Cohen's $d = -0.31$), but the difference between the groups was significant ($t_{57.78} = -2.24$, $p = .029$, Cohen's $d = -0.59$). This suggests a stronger signal-to-noise ratio during sadness detection in depression. However, because the mean correlations in each group were not significantly different from 0 (i.e., did not support the ability of the model to capture response time data), this result is weaker than that observed in the happiness condition.

Because correlation is scale and shift invariant, these results cannot be explained by a difference between groups in the mean or variability of response times. In addition, choice data did not differ significantly between groups (*t* tests, all $ps > .1$). For descriptive statistics of choice data, see the Supplement.

Invariant Processing of Sadness Across Changes in Identity Was Impaired in Depression

Comparison of the templates shown in Figure 3 across identities suggests that the features used for identification of happiness were invariant to changes in identity. In all identities, the key features were darkened areas around the oral commissures, which give the impression of a smile. This was

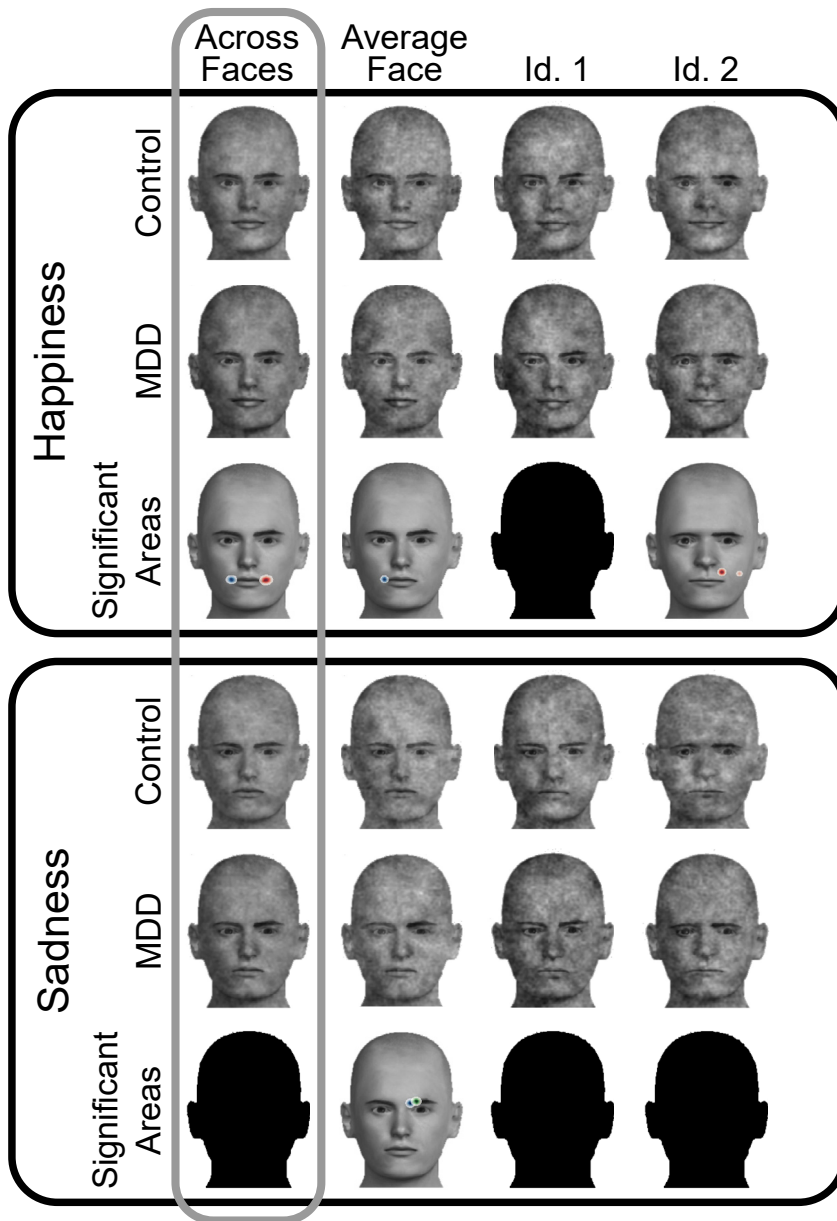


Figure 3. Estimated templates for the detection of happiness (top) and sadness (bottom). In each panel, the first 2 rows show the templates superimposed over base face images, and the last row shows the results of the cluster analysis, with significant clusters for the control group in red, for the major depressive disorder (MDD) group in blue, and significant differences in green. The main template estimated from all data is highlighted by the gray outline. Id, identity.

supported by the analysis of variance, which showed no effects of group ($F_{1,171} = 0.002, p = .964, \eta^2 = 0.000$; identity pair, $F_{2,171} = 0.056, p = .946, \eta^2 = 0.000$) or their interaction ($F_{2,171} = 0.45, p = .640, \eta^2 = 0.005$) on the similarity between templates.

On the other hand, the features used for identification of sadness did seem to change in the MDD group, with the template that was obtained at the average identity showing frowning (darkened brow) and raising of the left nostril/lip, which together give the impression of pain. This was absent from other templates, which consistently showed gaze down and lowering of the mouth commissures. Consistent with these observations, the analysis of variance showed a main effect of group ($F_{1,171} = 5.94, p = .016, \eta^2 = 0.03$) but no effect of identity pair ($F_{2,171} = 1.68, p = .189, \eta^2 = 0.02$) or their

interaction ($F_{1,171} = 0.33, p = .720, \eta^2 = 0.000$). The group effect suggests that the information used for recognition of sadness was less invariant to identity in participants with depression (mean correlation = 0.07) than in healthy control participants (mean correlation = 0.09).

DISCUSSION

We used reverse correlation to obtain estimates of the templates used by people with depression and healthy control participants in the detection of happiness and sadness. Using the estimated templates in a model-based analysis, we found evidence suggesting that depression is associated with a reduced signal-to-noise ratio in the detection of happiness.

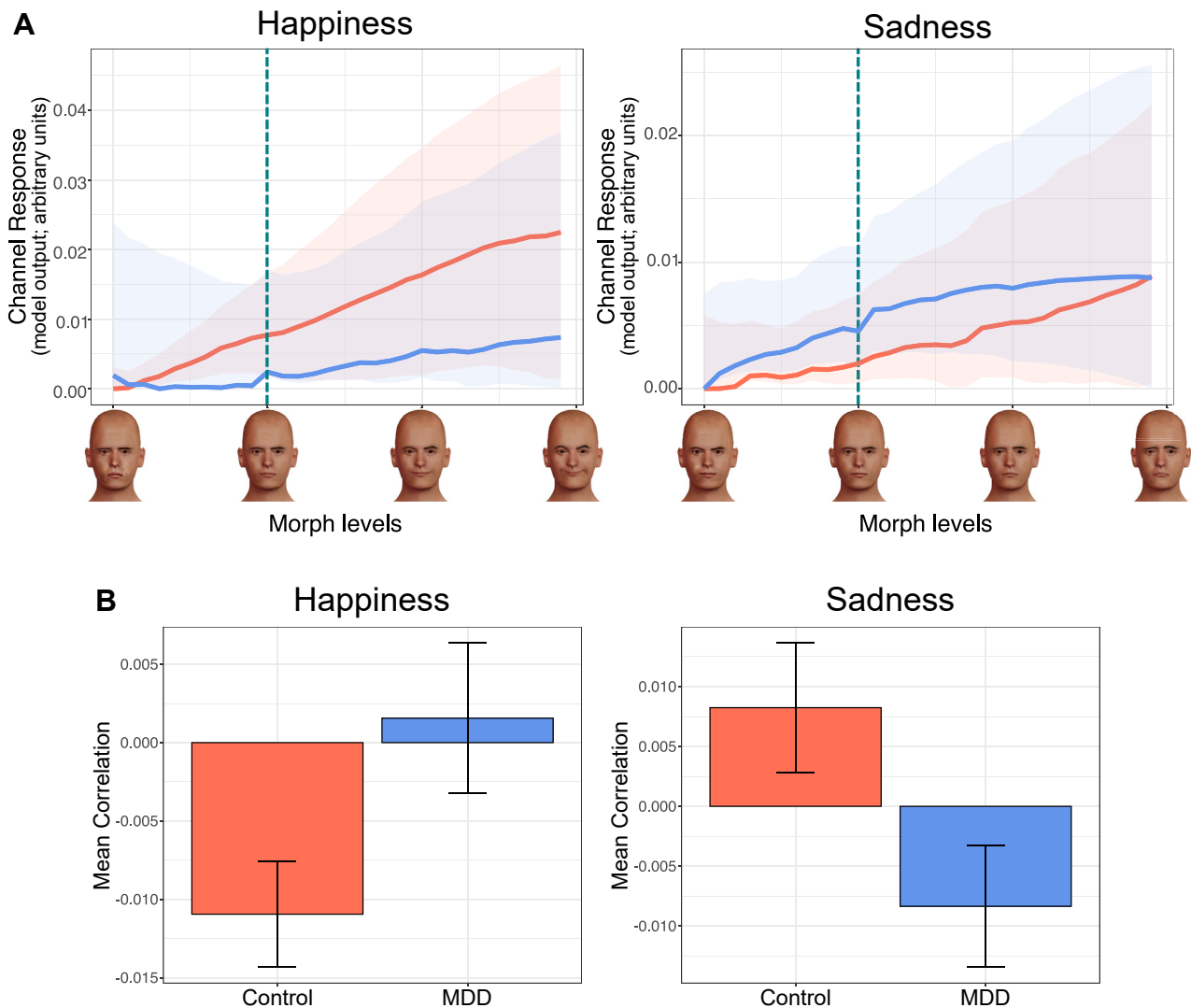


Figure 4. Results of model-based analyses. **(A)** Tuning curves from the selectivity analysis, and **(B)** mean correlations between sensory evidence variables and response times. Results from the major depressive disorder (MDD) group are shown in blue, and results from the control group are shown in red.

The happiness template produced predictions of sensory evidence that were less correlated with response times in people with depression than in healthy control participants. The opposite results were found for the detection of sadness, but nonsignificant correlations within each group suggest that the differences between groups should be interpreted with caution. Because opposite differences between groups were found depending on emotional expression, our results cannot be explained by a general effect of depression on perception, cognition, or performance.

We found little evidence that depression is accompanied by changes in selectivity for the detection of happiness or sadness. Notwithstanding these results, we do not believe that the selectivity hypothesis can be ruled out without additional research. Besides the observed significant differences, the areas that each group used for expression identification often

landed on different sides of the face. For example, significant clusters in the analysis of happiness were on the left side of the face for the control group but on the right side for the MDD group (see Figure 3). Furthermore, although differences in tuning functions obtained from the estimated models (Figure 4A) were not significant, their pattern was exactly what would be expected based on results from studies using signal detection analyses (15). Such results led to the hypothesis that face emotion deficits in depression can be explained by a reduction in the output of channels that process positive emotions (15). The interpretation of our results in terms of a reduction in signal-to-noise ratio for happiness is also consistent with such an explanation.

Previous research has shown that depression is accompanied by a reduction in sensitivity to positive outcomes either during learning or decision making (33–35). While we interpret

our results as being perceptual in nature, a body of research (36–38) links visual attention and reward learning implemented in the basal ganglia (39). It is possible that reinforcement learning mechanisms underlie face perception deficits in depression. Relatedly, depression may change people's exposure to various expressions (e.g., less exposure to happy faces), with the perceptual system adapting to such contingencies. Such learning hypotheses are important, but they are orthogonal to the question that we set out to answer here.

To the degree that degraded signal from positive affective stimuli (and increased signal from negative stimuli) contributes to the maintenance of depression, these results may provide useful treatment targets. Previous studies have suggested that antidepressants can alter the processing of emotional information (40), but no previous studies have used reverse correlation to test this possibility precisely. Furthermore, reduced signal to emotional information may also be a promising target for cognitive training paradigms, also known as cognitive bias modification (41). It could be quite informative to use a cognitive training paradigm to manipulate the signal-to-noise ratio during emotion detection and then determine whether depression symptoms subsequently improve. Current cognitive bias modification paradigms target attentional mechanisms, and their success may be due to the known role of attention in reducing internal noise (42,43). Perceptual learning is also known to reduce internal noise (44,45), with its effects quantified as being an order of magnitude stronger than those of attention (44), making perceptual learning a strong candidate for the development of improved cognitive bias modification paradigms.

Limitations

Several aspects of our methodology limit the generalizability of our results. We used 3-dimensional face models rather than naturalistic faces to achieve tight stimulus control, and we investigated only a few identities and expressions to ensure that there were enough trials for reverse correlation. More research will be necessary to test the generalizability of our results across changes in face stimuli. Our task was designed to efficiently estimate templates and may have low ecological validity.

Depression reduces sensitivity to emotional expression in faces in general, not just for expressions of happiness and sadness (11,12). More research is necessary to determine whether a lower signal-to-noise ratio may also be present in the processing of expressions other than happiness.

Depression and anxiety are highly comorbid (46). Because anxiety may also be accompanied by changes in perception of face expression (47), an open question is whether there are multiple perceptual mechanisms affected by mood and anxiety disorders, and if the answer is yes, how the distribution of changes is related to individual symptomatology. Only a combination of highly targeted studies, such as ours, and large-scale studies can answer these questions. The former refine our hypotheses about the mechanisms that underlie face perception in mood and anxiety disorders, and the latter produce a better understanding of how a person's symptomatology may lead to a specific pattern of changes in face perception.

Our analysis and interpretation of results are based on several assumptions. Because it is common in psychophysics,

our model-based analyses amalgamated perceptual and decisional sources of noise into a single construct of internal noise. The visual system is highly nonlinear, and the LOM should be considered only a first (linear) approximation to system identification (18). Finally, it is likely that the templates used by people for face perception are better characterized using facial features (48) rather than at the level of pixel luminance. Future research should focus more strongly on feature and texture spaces.

Finally, we did not assess history of medication use. How this and other variables might have influenced the results reported here are questions for future research.

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REFERENCES

1. Montague PR, Dolan RJ, Friston KJ, Dayan P (2012): Computational psychiatry. *Trends Cogn Sci* 16:72–80.
2. Wang XJ, Krystal JH (2014): Computational psychiatry. *Neuron* 84:638–654.
3. Huys QJM, Browning M, Paulus MP, Frank MJ (2021): Advances in the computational understanding of mental illness. *Neuropsychopharmacology* 46:3–19.
4. Plana I, Lavoie MA, Battaglia M, Achim AM (2014): A meta-analysis and scoping review of social cognition performance in social phobia, posttraumatic stress disorder and other anxiety disorders. *J Anxiety Disord* 28:169–177.
5. Gao Z, Zhao W, Liu S, Liu Z, Yang C, Xu Y (2021): Facial emotion recognition in schizophrenia. *Front Psychiatry* 12:633717.
6. Lozier LM, Vanmeter JW, Marsh AA (2014): Impairments in facial affect recognition associated with autism spectrum disorders: A meta-analysis. *Dev Psychopathol* 26:933–945.
7. Bora E, Pantelis C (2016): Meta-analysis of social cognition in attention-deficit/hyperactivity disorder (ADHD): Comparison with healthy controls and autistic spectrum disorder. *Psychol Med* 46:699–716.
8. Bora E, Zorlu N (2017): Social cognition in alcohol use disorder: A meta-analysis. *Addiction* 112:40–48.
9. Daros AR, Zakzanis KK, Rector NA (2014): A quantitative analysis of facial emotion recognition in obsessive-compulsive disorder. *Psychiatry Res* 215:514–521.

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10. Daros AR, Zakzanis KK, Ruocco AC (2013): Facial emotion recognition in borderline personality disorder. *Psychol Med* 43:1953–1963.
11. Bistricky SL, Ingram RE, Atchley RA (2011): Facial affect processing and depression susceptibility: Cognitive biases and cognitive neuroscience. *Psychol Bull* 137:998–1028.
12. Bourke C, Douglas K, Porter R (2010): Processing of facial emotion expression in major depression: A review. *Aust N Z J Psychiatry* 44:681–696.
13. Krause FC, Linardatos E, Fresco DM, Moore MT (2021): Facial emotion recognition in major depressive disorder: A meta-analytic review. *J Affect Disord* 293:320–328.
14. Dalili MN, Penton-Voak IS, Harmer CJ, Munafò MR (2015): Meta-analysis of emotion recognition deficits in major depressive disorder. *Psychol Med* 45:1135–1144.
15. Soto FA, Stewart RA, Hosseini S, Hays JS, Beevers CG (2021): A computational account of the mechanisms underlying face perception biases in depression. *J Abnorm Psychol* 130:443–454.
16. Lu ZL, Doshier B (2013): *Visual Psychophysics: From Laboratory to Theory*. Cambridge: MIT Press.
17. Abbey CK, Eckstein MP (2002): Classification image analysis: Estimation and statistical inference for two-alternative forced-choice experiments. *J Vis* 2:66–78.
18. Murray RF (2011): Classification images: A review. *J Vis* 11:2.
19. Murray RF (2012): Classification images and bubbles images in the generalized linear model. *J Vis* 12:2.
20. Knoblauch K, Maloney LT (2008): Estimating classification images with generalized linear and additive models. *J Vis* 8:10.1–1019.
21. Clark CM, Gosselin F, Goghari VM (2013): Aberrant patterns of visual facial information usage in schizophrenia. *J Abnorm Psychol* 122: 513–519.
22. Clark CM, Chiu CG, Diaz RL, Goghari VM (2014): Intact anger recognition in depression despite aberrant visual facial information usage. *J Affect Disord* 165:196–202.
23. Spezio ML, Adolphs R, Hurley RSE, Piven J (2007): Abnormal use of facial information in high-functioning autism. *J Autism Dev Disord* 37:929–939.
24. Rush AJ, Trivedi MH, Ibrahim HM, Carmody TJ, Arnow B, Klein DN, *et al.* (2003): The 16-Item Quick Inventory of Depressive Symptomatology (QIDS), clinician rating (QIDS-C), and self-report (QIDS-SR): A psychometric evaluation in patients with chronic major depression. *Biol Psychiatry* 54:573–583.
25. Sheehan DV, Lecrubier Y, Harnett Sheehan KH, Janavs J, Weiller E, Keskiner A, *et al.* (1997): The validity of the Mini International Neuropsychiatric Interview (MINI) according to the SCID-P and its reliability. *Eur Psychiatry* 12:232–241.
26. Hays JS, Wong C, Soto FA (2020): FaReT: A free and open-source toolkit of three-dimensional models and software to study face perception. *Behav Res Methods* 52:2604–2622.
27. Mangini MC, Biederman I (2004): Making the ineffable explicit: Estimating the information employed for face classifications. *Cogn Sci* 28:209–226.
28. Dotsch R (2015): rcicr: Reverse correlation image classification toolbox [R package], version 0.3.2.1. Available at: <https://github.com/rdotsch/rcicr>. Accessed October 1, 2023.
29. Smith SM, Nichols TE (2009): Threshold-free cluster enhancement: Addressing problems of smoothing, threshold dependence and localisation in cluster inference. *Neuroimage* 44:83–98.
30. MacGregor-Fors I, Payton ME (2013): Contrasting diversity values: Statistical inferences based on overlapping confidence intervals. *PLoS One* 8:e56794.
31. Aviezer H, Ensenberg N, Hassin RR (2017): The inherently contextualized nature of facial emotion perception. *Curr Opin Psychol* 17:47–54.
32. Soto FA (2019): Categorization training changes the visual representation of face identity. *Atten Percept Psychophys* 81:1220–1227.
33. Chen C, Takahashi T, Nakagawa S, Inoue T, Kusumi I (2015): Reinforcement learning in depression: A review of computational research. *Neurosci Biobehav Rev* 55:247–267.
34. Pike AC, Robinson OJ (2022): Reinforcement learning in patients with mood and anxiety disorders vs control individuals: A systematic review and meta-analysis. *JAMA Psychiatry* 79:313–322.
35. Robinson OJ, Chase HW (2017): Learning and choice in mood disorders: Searching for the computational parameters of anhedonia. *Comput Psychiatr* 1:208–233.
36. Anderson BA (2016): The attention habit: How reward learning shapes attentional selection. *Ann N Y Acad Sci* 1369:24–39.
37. Failing M, Theeuwes J (2018): Selection history: How reward modulates selectivity of visual attention. *Psychon Bull Rev* 25:514–538.
38. Le Pelley ME, Mitchell CJ, Beesley T, George DN, Wills AJ (2016): Attention and associative learning in humans: An integrative review. *Psychol Bull* 142:1111–1140.
39. Anderson BA (2019): Neurobiology of value-driven attention. *Curr Opin Psychol* 29:27–33.
40. Harmer CJ, Goodwin GM, Cowen PJ (2009): Why do antidepressants take so long to work? A cognitive neuropsychological model of antidepressant drug action. *Br J Psychiatry* 195:102–108.
41. Fodor LA, Georgescu R, Cuijpers P, Szamoskozi Ş., David D, Furukawa TA, Cristea IA (2020): Efficacy of cognitive bias modification interventions in anxiety and depressive disorders: A systematic review and network meta-analysis. *Lancet Psychiatry* 7:506–514.
42. Lu ZL, Doshier BA (1998): External noise distinguishes attention mechanisms. *Vision Res* 38:1183–1198.
43. Ling S, Liu T, Carrasco M (2009): How spatial and feature-based attention affect the gain and tuning of population responses. *Vision Res* 49:1194–1204.
44. Doshier BA, Lu ZL (1998): Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proc Natl Acad Sci U S A* 95:13988–13993.
45. Doshier BA, Lu ZL (1999): Mechanisms of perceptual learning. *Vision Res* 39:3197–3221.
46. Kessler RC, Walters EE (1998): Epidemiology of DSM-III-R major depression and minor depression among adolescents and young adults in the national comorbidity survey. *Depress Anxiety* 7:3–14.
47. Günther V, Kropidowski A, Schmidt FM, Koelkebeck K, Kersting A, Suslow T (2021): Attentional processes during emotional face perception in social anxiety disorder: A systematic review and meta-analysis of eye-tracking findings. *Prog Neuropsychopharmacol Biol Psychiatry* 111:110353.
48. Valentine T, Lewis MB, Hills PJ (2016): Face-space: A unifying concept in face recognition research. *Q J Exp Psychol (Hove)* 69:1996–2019.