



Congenital Anosmia and Facial Emotion Recognition

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ABSTRACT

Major functions of the olfactory system include guiding ingestion and avoidance of environmental hazards. People with anosmia report reliance on others, for example to check the edibility of food, as their primary coping strategy. Facial expressions are a major source of non-verbal social information that can be used to guide approach and avoidance behaviour. Thus, it is of interest to explore whether a life-long absence of the sense of smell heightens sensitivity to others' facial emotions, particularly those depicting threat. In the present, online study 28 people with congenital anosmia (mean age 43.46) and 24 people reporting no olfactory dysfunction (mean age 42.75) completed a facial emotion recognition task whereby emotionally neutral faces (6 different identities) morphed, over 40 stages, to express one of 5 basic emotions: anger, disgust, fear, happiness, or sadness. Results showed that, while the groups did not differ in their ability to identify the final, full-strength emotional expressions, nor in the accuracy of their first response, the congenital anosmia group successfully identified the emotions at significantly lower intensity (i.e. an earlier stage of the morph) than the control group. Exploratory analysis showed this main effect was primarily driven by an advantage in detecting anger and disgust. These findings indicate the absence of a functioning sense of smell during development leads to compensatory changes in visual, social cognition. Future work should explore the neural and behavioural basis for this advantage.

1. Introduction

The major functions of the olfactory system are to guide ingestion and avoidance of environmental hazards, such as fire or decayed food [31]. Indeed, people with olfactory loss report a higher incidence of household accidents and cite concerns about safety and hygiene as the major consequences of living without a sense of smell [3,4,29]. Various coping strategies are reported by people with anosmia, primarily involving reliance on others, for example to check food [2,21].

In addition to explicit spoken exchanges, humans utilize non-verbal cues from others to respond adaptively to their environment [10]. Facial expressions are one key source of social information that can be used to guide approach and avoidance behaviour [14]. The sense of smell also plays a significant, though largely unconscious role in social communication [31]. Indeed, as one of the first senses to develop, it has been proposed that olfaction scaffolds an infant's social learning, with maternal odour capturing and guiding attention towards faces, as well as regulating physiological responses to threat [28]. Social odour cues can also influence adults' perceptions of faces [5]. For example, non-conscious exposure to male axillary odour has been reported to

enhance women's attractiveness ratings of male faces [32]. Furthermore, a range of studies report exposure to axillary odour, collected under either positive or negative emotional states, selectively modulates the receiver's detection of facial emotions [5]. For example, exposure to anxiety odour disrupted emotional priming of happy faces [22], while fear body odour biased participants toward interpreting ambiguous facial expressions as more fearful [6,34].

Given people with congenital anosmia report reliance on others as their primary strategy to avoid environmental hazards, it is of interest to explore whether they show heightened sensitivity to others' facial emotions, particularly those depicting threat [19], or whether a lack of olfactory scaffolding during development has had a lasting detrimental effect on their social-cognitive skills [28]. Enhanced acuity and neural reorganisation have been widely reported in those with a congenital absence of visual or auditory input [1,20]. Though much less widely studied, there is some evidence that congenital anosmia is also associated with enhanced processing in other (multi)sensory domains [23,24]. Neurally, this appears to reflect enhanced processing in multisensory brain regions [23], including the posterior superior temporal sulcus (pSTS), an area with established roles in both audio-visual binding and

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processing of dynamic aspects of facial expressions [30].

Initial behavioural support for the sensitivity enhancement hypothesis comes from a study where participants viewed faces as they morphed from neutral to express one of 6 basic emotions (Anger, Sadness, Fear, Disgust, Surprise and Happiness). Congenitally anosmic participants made fewer errors at identifying disgust and fear expressions than controls [19], while the error rates of an additional, acquired anosmia group correlated negatively with the duration of their olfactory loss. The authors interpret these findings as reflecting a compensatory effect of the anosmic participants' inability to detect environmental hazards through odours, manifested as increased sensitivity to the non-verbal social cues of others. Despite this intriguing finding, to our knowledge, no other studies have explored compensatory effects of olfactory loss on social-cognitive functioning [29].

Thus, the aim of the present study was to replicate and extend this initial study [19], comparing performance of a new group of congenitally anosmic participants to a group of age matched controls with intact olfactory function. With only $N = 17$ congenitally anosmic participants, the original study was somewhat underpowered [19], as is typical given the difficulty of recruiting a group with a rather rare condition [3]. Therefore here, in attempt to recruit a larger sample, we conducted the study online, using a version of the same behavioural task [19,26]. In addition, in order to test the generalisability of the previous finding, while Lemogne et al.'s study used face stimuli from Eckman's widely cited Facial Affect Series [9], here we used stimuli from more modern, naturalistic, freely available database [8], with stimuli varying by age and gender. It was hypothesised that, in-line with the previous report, congenitally anosmic participants would show greater sensitivity to the detection of facial emotions, particularly those signalling potential threat, as they evolved from neutral to express a range of basic emotions.

2. Methods

2.1. Participants

28 participants aged 20–65 ($M = 43.46$, $SD = 12.48$, 21 Female), self-reporting congenital anosmia, were recruited via the closed Facebook group *Congenital Anosmia*. 35.7 % of the congenital anosmia group were based in Great Britain, 39.2 % in North America, 10.7 % in Europe, 7.14 % in Asia and 3.6 % South America.

24 participants aged 21–66 ($M = 42.75$, $SD = 16.49$, 14 Female), self-reporting no olfactory dysfunction were recruited from the friends and family of the Congenital Anosmia (CA) group and via student networks at Liverpool John Moores University. 87.5 % of the control group were based in Great Britain and 12.5 % in North America.

Exclusion criteria for both groups were being under 18 or over 70 years of age, acquired anosmia, parosmia, traumatic brain injury and any visual impairment not corrected by glasses. The study was approved by LJMU's Psychology Research Ethics Committee.

2.2. Measures

2.2.1. Olfactory ability

Participants were asked to self-report olfactory ability (1 = congenital anosmia, 2 = acquired anosmia, 3 = long-term acquired anosmia, 4 = never experienced smell loss/ only temporarily). They were also asked to rate their self-perceived olfactory function on a visual analogue scale, with 0 = no ability to smell, and 100 = perfect sense of smell (Zou et al., 2019).

In addition, participants were provided with a list of 5 household items (Ground coffee/Coffee granules, Orange/ Lemon rind, A dab of toothpaste, A drop of washing up liquid, Mustard/ Ketchup/ Brown sauce) and asked to "please smell the items you have available and mark on the scale the extent to which you can smell them (based on <https://abscent.org/learn-us/smell-training/self-assessment>). 1. I'm not aware of the smell at all. 2. I'm aware of something very, very faint, but

that's all. 3. I can smell something, but it doesn't make sense to me. 4. The item smells very distorted and unpleasant to me. 5. I am able to identify the smell. If they didn't have access to the item, they were asked to leave the response empty.

2.2.2. State trait anxiety inventory (STAI)

The STAI, developed by Spielberger (1983) includes separate measures of state and trait anxiety. The State-Anxiety scale (STAI) consists of 20 statements that evaluate how respondents feel *right now, at this moment* while the Trait-anxiety scale consists of twenty statements that assess how people *generally feel*. On both scales, responses range from 1 (Not at all) to 4 (Very much so). Scores range from 20 to 80, with higher scores indicating greater anxiety.

2.2.3. Facial emotion recognition task (FERT)

The FERT consisted of 36 trials presented in a random order [26]. Trials began with a 1000msec fixation cross followed by a neutral face which morphed into one of 5 emotions (anger, disgust, fear, happiness, and sadness) over 40 frames, i.e. 2.5 % incremental stages. Each frame was shown for 500 ms, with a morph evolving over 20 s. 6 facial identities were shown (3 men, 3 women), from 3 age groups (old, middle-aged, and young) each expressing 5 emotions in total. Faces were taken from the FACES database (<https://faces.mpg.de/imeji/>) and morphs created using Morpheus photo morpher (<http://www.morpheussoftware.net/>). See Fig. 1 for exemplars.

Participants were asked to report the emotion as soon as they were confident in their choice, rather than guessing, by clicking the corresponding box, located below the image. Participants were informed that they could change their response as often as necessary. At the end of each trial, participants were presented with the static, full-strength emotion and asked to make their final selection of which emotion was shown, using a 5AFC response (coded as stage 41). This screen remained until participants made their final response.

Three scores were computed for each emotion: 1. The final success rate (i.e., the percentage of correct responses at the 41st stage), 2. The percentage of trials where the first response was accurate, 3. The number of stages required to accurately identify the emotion (on a scale of 1–41). The task was programmed in PsychoPy version 22.2.5 (<https://www.psychopy.org/>) and run online via Pavlovia (<https://pavlovia.org/>). See Fig. 2 for task diagram.

2.3. Procedure

Participants first followed a link to an online survey hosted on QuestionPro. Here they were presented with a participant information sheet followed by a series of screening questions to ensure they met the study inclusion criteria. After a series of demographic questions, they completed the state-trait anxiety inventory, followed by the smell self-assessment test. Upon completion of this, participants were re-routed to Pavlovia where they completed the emotion recognition task. Finally, participants were provided with a debrief sheet which summarised the aims of the study.

2.4. Data processing and analysis

Data were extracted as CSV files from QuestionPro and Pavlovia and matched up using a unique participant ID which was automatically generated at the start of the survey. Only participants with full data sets were considered to have completed the study.

Initial screening of the data revealed that some participants rarely made any responses during the morph stage of the task and only responded at the forced choice questions. Across the study sample, the mean number of such response omissions was 4.38 trials ($SD 7.6$). However, 4 participants, 2 from each group, had omissions > than 2SD above the mean (omissions on 24, 26, 26, and 26 out of 36 trials). All these participants omitted responses on 50 % or more of the Happy

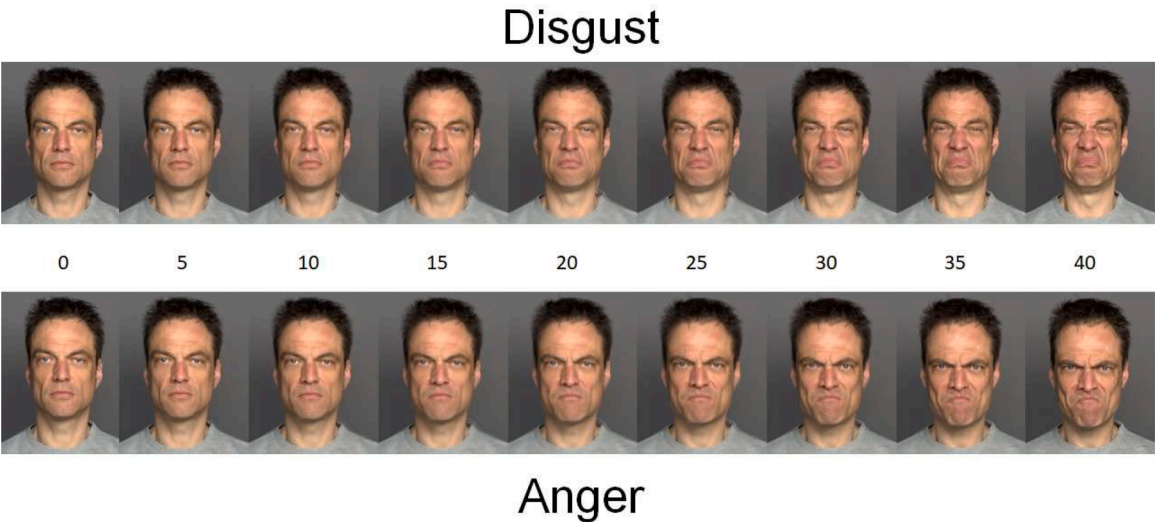


Fig. 1. Exemplar morphs from neutral (0) to full emotion (40) for disgust and anger. Both emotions share brow knitting but later emerging differences in the nose and mouth region ultimately differentiate them [15].

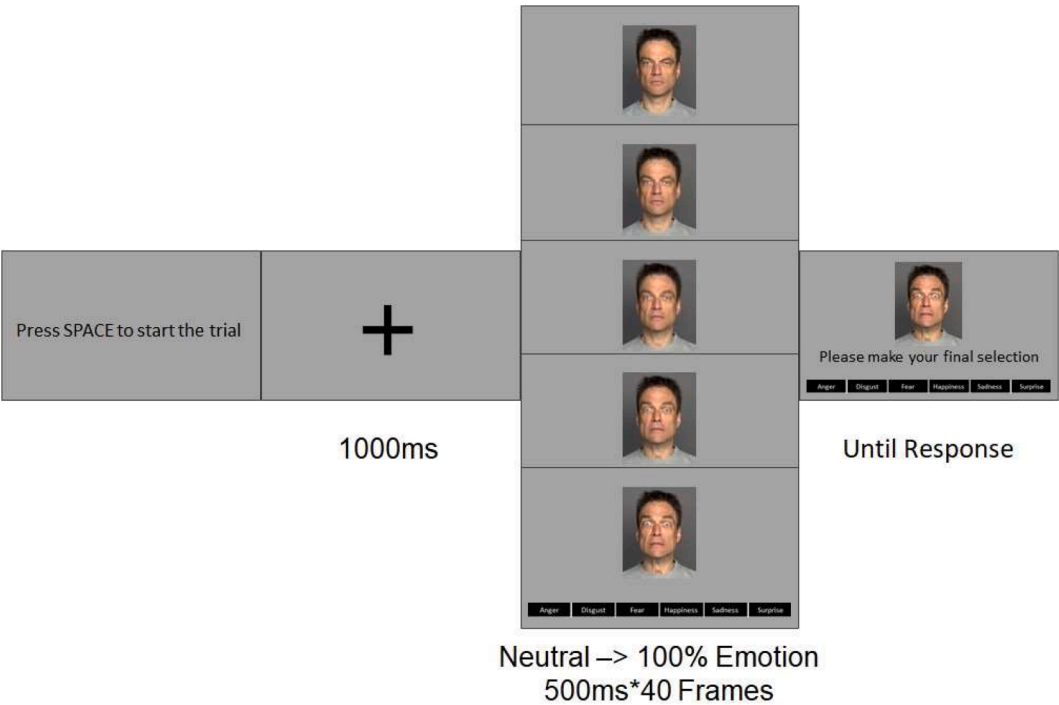


Fig. 2. Task-trial diagram. Participants completed 30 trials (6 facial identities * 5 emotions). Each trial started with a 1000msec fixation cross and then a face morphed from neutral to full emotion over 40 frames, with each frame presented for 500 ms (20 s per trail). Participants could respond at any time during the morph and change their mind if they decided an earlier response was incorrect. The final screen on each trial presented the full-strength emotion again and participants confirmed their final selection.

trials, which were the easiest and where mean omissions were only 0.65 trials (SD 1.43). Therefore, it was concluded these participants hadn't engaged with the task as instructed and were excluded from the final analysis. N.B. Their inclusion makes no substantive difference to the results reported. Demographic data for the final study sample are shown in Table 1.

Data were analysed using SPSS (version 27 – IBM). Independent samples *t*-tests were used to compare groups on key demographics: age, anxiety, and self-reported olfactory function. Equality of variances were assessed using Levene's test. A series of mixed ANOVAs - Group (CA, Control) * Emotion type (Happy, Sad, Anger, Disgust, Fear) were used to

Table 1		
Descriptive statistics showing group means (SD) for age, anxiety, and self-reported olfactory function.		
Variable	Congenital Anosmia	Control Group
Age (years)	42.85 (12.7)	42.45 (16.1)
State Anxiety	36.38 (11.35)	34.77 (10.00)
Trait Anxiety	40.23 (12.66)	41.00 (8.89)
Functional Rating	3.61 (10.23)	83.59 (9.77)
Self-Assessment	5.54 (1.21)	23.82 (2.82)

compare performance on each of the 3 outcome measures. Where assumptions of sphericity were violated, as indicated by Mauchly's test, Greenhouse-Geisser correction was applied. Main effects of interest were followed up with pairwise comparisons where appropriate. Bonferroni correction was applied to adjust for multiple comparisons.

3. Results

Descriptive statistics are presented in Table 1. There were no significant differences between the two groups in terms of their age or scores on the State and Trait Anxiety scales (All $t_s < 1$, all $p_s > 0.6$).

As would be expected, the CA group rated their olfactory function significantly lower than the control group, $t(46) = 27.54$, $p < .001$. There were only 2 missing ratings on the olfactory self-assessment across the whole sample; one person from each group omitted orange / lemon rind. Ratings (1–5) for each item were totalled to give an overall self-assessment score. Thus, a total score of 5 indicates no detection of any smell and a total score of 25 indicates confidence they could identify all of the items. Means and SDs are shown in Table 1. As anticipated, most ratings in the CA group were 1. The highest total score in the CA group was 10, this participant rated all items as 2, "I'm aware of something very, very faint, but that's all". The lowest total score in the control group was 17. This person rated 3 of the 5 items as 5 (coffee, lemon / orange rind and mustard) but reported no sensation from washing up liquid or toothpaste. The differences between the two groups were statistically significant, $t(46) = 28.27$, $p < .001$.

Accuracy identifying final, full emotion.

There was a significant main effect of Emotion, $F(4,184) = 24.94$, $p < .001$, partial $\eta^2 = 0.352$. Pairwise comparisons with Bonferroni correction revealed that Happy faces were identified more accurately than any other emotion (all $p_s \leq .002$). Fear and Sadness were the next most accurately recognised, with both being identified significantly more accurately than Disgust or Anger (all $p_s < 0.03$). Disgust and Anger were the least accurately identified and performance on these trials did not differ to each other ($p = 1$) (Fig. 3).

There was no significant main effect of Group, $F(1,46) = 0.31$, $p = .58$, partial $\eta^2 = 0.007$. Nor was there a significant Emotion x Group interaction, $F(4,184) = 0.92$, $p = .45$, partial $\eta^2 = 0.02$ (Fig. 3).

Accuracy on first guess.

There was a significant main effect of Emotion, $F(4,184) = 17.84$, $p < .001$, partial $\eta^2 = 0.28$. This reflects the fact first responses on Happy

trials were significantly more accurate than first responses for any other emotion, $p_s < 0.001$. First response accuracy didn't differ between any of the other emotions (Fig. 4).

There was no significant main effect of Group, $F(1,46) = 0.0001$, $p = .996$, partial $\eta^2 = < 0.001$. Nor was there a significant Group X Emotion interaction, $F(4,184) = 0.095$, $p = .98$, partial $\eta^2 = 0.002$ (Fig. 4).

Mean number of phases required for correct recognition.

There was a significant main effect of Emotion, $F(4,184) = 53.88$, $p < .001$ partial $\eta^2 = 0.54$. Pairwise comparisons demonstrated this reflects the fact Happiness was identified significantly earlier than any of the other emotions, $p_s < 0.001$ (Fig. 5).

There was also a significant main effect of Group, $F(1,46) = 5.82$, $p = .02$, partial $\eta^2 = 0.11$. The CA group identified all emotions significantly earlier than the Control group. There was no significant Emotion x Group interaction, $F(4,184) = 1.51$, $p = .2$, partial $\eta^2 = 0.03$ (Fig. 5).

Exploratory analysis

Despite of the lack of significant interaction, given a previous study reported greater sensitivity among congenitally anosmic participants in identifying disgust and fear, we conducted post-hoc pairwise comparisons to determine whether the CA group showed a greater advantage over the Control group identifying some emotions than others. This revealed that the CA group identified both Disgust ($t(46) = 3.29$, $p = .002$) and Anger ($t(46) = 2.59$, $p = .01$) significantly earlier than the Control group. There was a trend for the CA group to recognise Sadness significantly earlier than the Control group, $t(46) = 2.00$, $p = .05$. There were no differences between the two groups in stage of identification of the other two emotions (Happiness & Fear), $t_s < 2$, $p_s > 0.12$ (Fig. 5).

4. Discussion

In the present study the CA group were able to identify basic facial emotions at a lower threshold than an age matched control group who self-reported a healthy sense of smell. While the groups did not differ in their ability to identify full intensity, static emotions, people with a lifelong absence of the sense of smell were able to detect all emotions at an earlier stage of a dynamic morph than the control group. This heightened sensitivity was seen in the absence of any difference in the accuracy of the first responses made by the two groups, suggesting the findings reflect heightened sensitivity rather than incidental differences

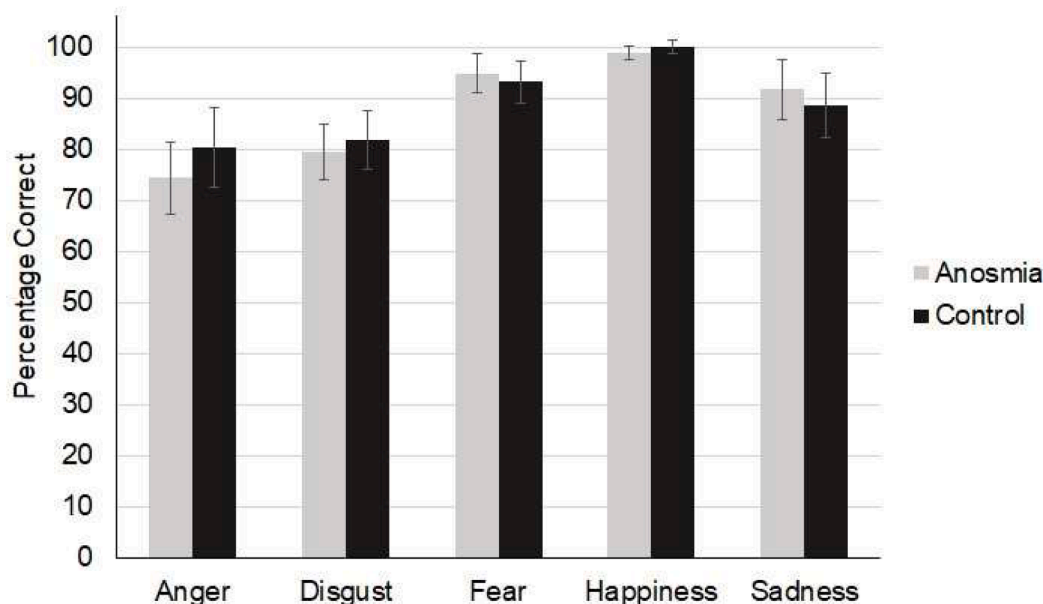


Fig. 3. Mean final recognition rate, presented as percentage correct for each emotion. Happy faces were identified significantly more accurately than any other emotion ($p_s \leq .002$). Fear and Sadness were identified significantly more accurately than Anger and Disgust ($p_s < 0.03$). Error Bars = 95 % CI.

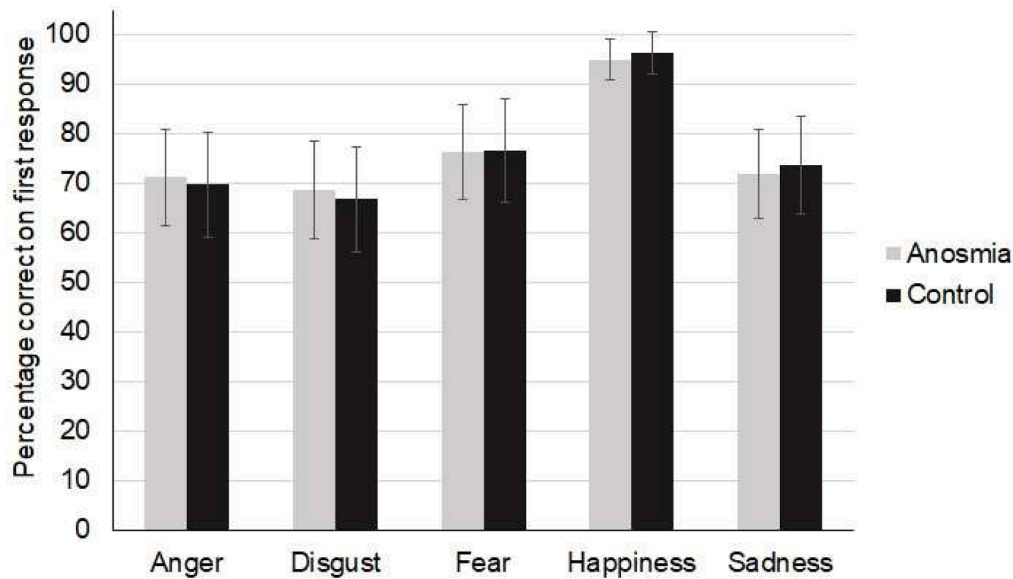


Fig. 4. Mean percentage of first responses that were correct for each emotion. First responses on Happy trials were significantly more accurate than for any other emotion, $p < 0.001$. Error Bars = 95 % CI.

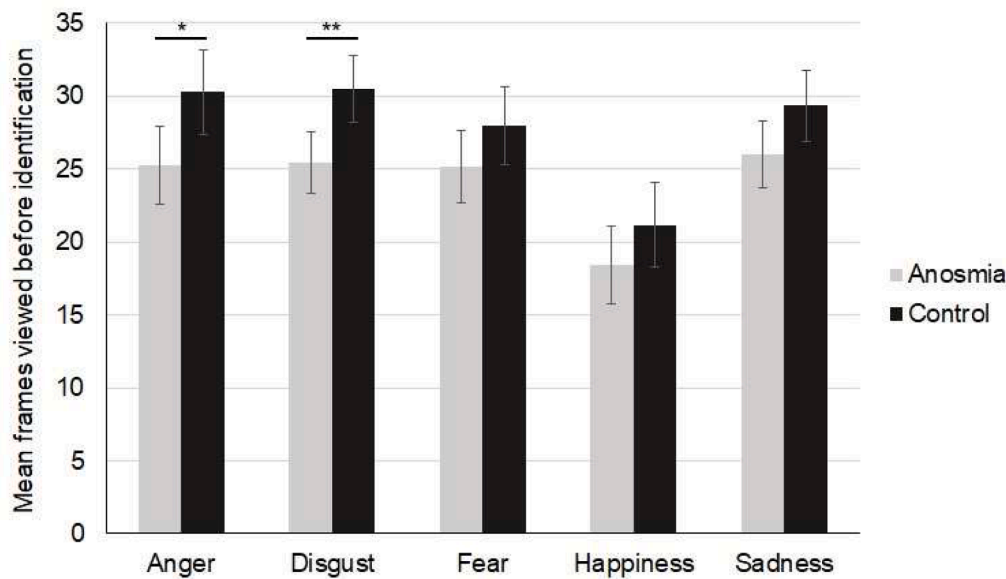


Fig. 5. Mean number of frames viewed before correct recognition of each emotion morph (0–41). There was a significant main effect of Emotion, with Happiness identified significantly earlier than any other, $p < 0.001$. There was a significant main effect of Group, with the CA group identifying all emotions earlier than the control group. Post-hoc pairwise comparisons revealed significantly earlier identification of Anger and Disgust. $*p = .01$, $**p = .002$. Error Bars = 95 % CI.

in response strategy. Exploratory post-hoc analysis indicated the anosmic advantage was primarily driven by superiority in detecting anger and disgust. While high sensitivity to expressions of disgust is likely to be particularly important to people with anosmia, the fact that anger and disgust were the hardest two expressions to identify and there was no anosmic advantage in the detection of fear, another highly relevant warning expression, means it isn't possible to conclude that the heightened sensitivity is emotion specific.

These findings are partially consistent with a previous study, using the same facial morphing task, which found people with congenital anosmia were more accurate at identifying fear and disgust, making fewer errors on their first response, than the control group [19]. However, in contrast to the present findings, this apparent advantage did not extend to identifying the emotions at an earlier stage of the morph. In

fact, the congenital anosmia group identified all emotions at a later stage, on average, than the control group, suggesting they may have been employing a more conservative response strategy than the control group. Such a response bias could reflect the fact testing was conducted in a clinical setting where demand characteristics meant accuracy was prioritised. While in the present study, the task instruction was for participants to respond when they knew the emotion rather than to guess, the home testing environment may have resulted in CA participants feeling comfortable making earlier responses.

There are also several methodological alterations between the present study and the previous one which could explain the differing findings. Firstly, while the original study used a classic set of facial affect stimuli [9], to test the generalisability of the original findings, here the dynamic emotion morphs were generated from a more modern, colour

set of previously validated facial emotion stimuli [8]. Additionally, only 5 of the basic emotions were included in the present study; given surprise is an affectively ambiguous emotion, identification of which did not interact with group in the previous study, it was omitted here. This omission reduced the length of time the task took to complete and increased power to detect effects of interest in the analysis. Consequently, participants also had fewer options to choose between, potentially making the task easier. However, performance levels of the control group in the present study, in terms of overall accuracy, initial error rate and average stage of emotion recognition, are comparable to the control group's performance in the previous study [19]. Thus, it seems unlikely fundamental differences in task difficulty explain the divergent results.

Given the challenges of recruiting congenitally anosmic participants in a limited geographical area, the present study was conducted online with the anosmic participants recruited, with permission, from a closed Facebook group, which one of the authors (JD) is a member of. While this resulted in a larger sample than the previous study, it comes with limitations in the characterisation and verification of both groups' olfactory function. COVID-19 induced olfactory loss has led to a rise in the use of at-home olfactory tests in research [33], one of which we included as a self-report screen for both groups. However, given that self-assessment of olfactory function can be unreliable [25] future, laboratory-based replication of this study, incorporating structural and functional screening of olfactory function, would add weight to the reported results.

Anxiety and depression have previously been reported to affect emotion recognition abilities [7,17]. In the previous study, the congenital anosmia group had significantly higher levels of self-reported anxiety and depression than the control group and this was accounted for in their statistical analysis [19]. Here, we found no differences between the groups in either state or trait anxiety. We did not include a separate measure of depression. However, given scores on the STAI are generally highly correlated with depression levels [16], it seems unlikely that the present findings were in fact driven by group differences in negative affectivity.

The present study is one of the first to explore whether there are compensatory effects of congenital anosmia on visual social-cognitive functioning. While the findings indicate heightened sensitivity to identification of basic facial emotions, which fits with first hand accounts of greater reliance on others for detection of environmental hazards [2,21], it doesn't offer insight into the mechanisms underlying this apparent advantage. Previous studies have reported enhanced audio-visual integration in congenital anosmia, which is reflected neurally as heightened activity in multisensory brain regions including the pSTS [23,24]. The pSTS is involved in the identification of dynamic facial expressions [30], offering a putative neural basis for the observed effects. Cultural differences in sensitivity to the detection and discrimination of different facial emotions have been reported to reflect differences in eye-gaze, with east Asian cultures attending more to the eye than the mouth region [11,12]. This strategy results in reduced sensitivity to the discrimination of anger and disgust, two emotions which share brow knitting early in their evolution with later emerging differences in the nose and mouth region ultimately differentiating them [13]. Thus, selective attention to key facial regions at different stages of the facial emotion's evolution could confer a detection advantage for the CA group. Theories of embodied cognition have proposed that facial emotion recognition relies at least in part on mimicry of others' facial expressions [27]. With previous studies reporting that recognition of dynamic expressions of facial emotions is predicted by the degree to which observers implicitly mimic the evolving pattern of facial muscle activity, as measured using facial EMG [18]. Future studies could evaluate these differing mechanistic explanations.

In conclusion, the present study adds to the limited existing evidence that, in-line with the enhanced acuity and behavioural compensation in congenital loss of vision and audition, anosmia too leads to a processing advantage in other sensory domains. Specifically, enhanced sensitivity

to the detection of evolving facial emotions, an important non-verbal cue guiding approach and avoidance behaviour. Future work is required to determine the behavioural and neural mechanisms underlying the reported effects.

CRediT authorship contribution statement

James Drummond: Writing – review & editing, Investigation, Formal analysis, Data curation, Conceptualization. **Adarsh Makdani:** Writing – review & editing, Software, Methodology, Data curation. **Ralph Pawling:** Writing – review & editing, Software, Methodology. **Susannah C. Walker:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Visualization, Writing – original draft.

Declarations of competing interest

None

Data availability

Data will be made available on request.

References

- [1] D. Bavelier, M.W.G. Dye, P.C. Hauser, Do deaf individuals see better? *Trends Cogn. Sci. (Regul. Ed.)* 10 (11) (2006) 512–518, <https://doi.org/10.1016/j.tics.2006.09.006>.
- [2] E.H. Blomqvist, A. Brämerson, P. Stjärne, S. Nordin, Consequences of olfactory loss and adopted coping strategies, *Rhinology* 42 (4) (2004) 189–194.
- [3] I. Croy, S. Negoias, L. Novakova, B.N. Landis, T. Hummel, Learning about the functions of the olfactory system from people without a sense of smell, *PLoS. One* 7 (3) (2012), <https://doi.org/10.1371/journal.pone.0033365>.
- [4] I. Croy, S. Nordin, T. Hummel, Olfactory disorders and quality of life—an updated review, *Chem. Senses* 39 (3) (2014) 185–194, <https://doi.org/10.1093/chemse/bjt072>.
- [5] F. Damon, N. Mezrai, L. Magnier, A. Leleu, K. Durand, B. Schaal, Olfaction in the Multisensory Processing of Faces: a Narrative Review of the Influence of Human Body Odors, *Front. Psychol.* 12 (October) (2021) 1–17, <https://doi.org/10.3389/fpsyg.2021.750944>.
- [6] J.H.B. de Groot, P.A. Kirk, J.A. Gottfried, Titrating the Smell of Fear: initial Evidence for Dose-Invariant Behavioral, Physiological, and Neural Responses, *Psychol. Sci.* 32 (4) (2021) 558–572, <https://doi.org/10.1177/0956797620970548>.
- [7] L.R. Demenescu, R. Korteakas, J.A. den Boer, A. Aleman, Impaired attribution of emotion to facial expressions in anxiety and major depression, *PLoS. One* 5 (12) (2010), <https://doi.org/10.1371/journal.pone.0015058>.
- [8] N.C. Ebner, M. Riediger, U. Lindenberger, FACES—a database of facial expressions in young, middle-aged, and older women and men: development and validation, *Behav. Res. Methods* 42 (1) (2010) 351–362, <https://doi.org/10.3758/BRM.42.1.351>.
- [9] P. Eckman, W.V. Friesen, *Pictures of Facial Affect*, Consulting Psychologists Press, Palo Alto, CA, 1976.
- [10] J. Hall, T. Horgan, N. Murphy, Nonverbal communication, *Annu. Rev. Psychol.* 70 (2019) 271–294, <https://doi.org/10.1146/annurev-psych-010418-103145>.
- [11] R.E. Jack, Culture and facial expressions of emotion, *Vis. cogn.* 21 (9–10) (2013) 1248–1286, <https://doi.org/10.1080/13506285.2013.835367>.
- [12] R.E. Jack, C. Blais, C. Scheepers, P.G. Schyns, R. Caldara, Cultural Confusions Show that Facial Expressions Are Not Universal, *Current Biology* 19 (18) (2009) 1543–1548, <https://doi.org/10.1016/j.cub.2009.07.051>.
- [13] R.E. Jack, O.G.B. Garrod, P.G. Schyns, Dynamic facial expressions of emotion transmit an evolving hierarchy of signals over time, *Current Biology* 24 (2) (2014) 187–192, <https://doi.org/10.1016/j.cub.2013.11.064>.
- [14] R.E. Jack, P.G. Schyns, The Human Face as a Dynamic Tool for Social Communication, *Current Biology* 25 (14) (2015) R621–R634, <https://doi.org/10.1016/j.cub.2015.05.052>.
- [15] R.E. Jack, W. Sun, I. Delis, O.G.B. Garrod, P.G. Schyns, Four not six: revealing culturally common facial expressions of emotion, *Journal of Experimental Psychology: General* 145 (6) (2016) 708–730, <https://doi.org/10.1037/xge0000162>.
- [16] K.A. Knowles, B.O. Olatunji, Specificity of trait anxiety in anxiety and depression: meta-analysis of the State-Trait Anxiety Inventory, *Clin. Psychol. Rev.* 82 (2020) 1–49, <https://doi.org/10.1016/j.cpr.2020.101928>.
- [17] F.C. Krause, E. Linardatos, D.M. Fresco, M.T. Moore, Facial emotion recognition in major depressive disorder: a meta-analytic review, *J. Affect. Disord.* 293 (December 2020) (2021) 320–328, <https://doi.org/10.1016/j.jad.2021.06.053>.

- [18] J. Künecke, A. Hildebrandt, G. Recio, W. Sommer, O. Wilhelm, Facial EMG responses to emotional expressions are related to emotion perception ability, *PLoS. One* 9 (1) (2014), <https://doi.org/10.1371/journal.pone.0084053>.
- [19] C. Lemogne, J. Smadja, E.H. Zerdazi, Y. Soudry, M. Robin, S. Berthoz, P. Bonfils, Congenital anosmia and emotion recognition: a case-control study, *Neuropsychologia* 72 (2015) 52–58, <https://doi.org/10.1016/j.neuropsychologia.2015.04.028>.
- [20] N. Lessard, M. Paré, F. Lepore, M. Lassonde, Early-blind human subjects localize sound sources better than sighted subjects, *Nature* 395 (6699) (1998) 278–280, <https://doi.org/10.1038/262228>.
- [21] S. Nordin, E. Hedén Blomqvist, P. Olsson, P. Stjärne, A. Ehnage, Effects of smell loss on daily life and adopted coping strategies in patients with nasal polyposis with asthma, *Acta Otolaryngol.* 131 (8) (2011) 826–832, <https://doi.org/10.3109/00016489.2010.539625>.
- [22] B.M. Pause, A. Ohrt, A. Prehn, R. Ferstl, Positive emotional priming of facial affect perception in females is diminished by chemosensory anxiety signals, *Chem. Senses* 29 (9) (2004) 797–805, <https://doi.org/10.1093/chemse/bjh245>.
- [23] M.G. Peter, G. Mårtensson, E.M. Postma, L. Engström Nordin, E. Westman, S. Boesveldt, J.N. Lundström, Seeing Beyond Your Nose? The Effects of Lifelong Olfactory Sensory Deprivation on Cerebral Audio-visual Integration, *Neuroscience* 472 (2021) 1–10, <https://doi.org/10.1016/j.neuroscience.2021.07.017>.
- [24] M.G. Peter, D.K. Porada, C. Regenbogen, M.J. Olsson, J.N. Lundström, Sensory loss enhances multisensory integration performance, *Cortex* 120 (2019) 116–130, <https://doi.org/10.1016/j.cortex.2019.06.003>.
- [25] C.M. Philpott, C.R. Wolstenholme, P.C. Goodenough, A. Clark, G.E. Murty, Comparison of subjective perception with objective measurement of olfaction, *Otolaryngology—Head and Neck Surgery*, 134 (3) (2006) 488–490.
- [26] M. Robin, A. Pham-Scottez, F. Curt, C. Dugre-Le Bigre, M. Speranza, D. Sapinho, G. Kedia, Decreased sensitivity to facial emotions in adolescents with Borderline Personality Disorder, *Psychiatry Res.* 200 (2–3) (2012) 417–421, <https://doi.org/10.1016/j.psychres.2012.03.032>.
- [27] K. Rymarczyk, Ł. Zurawski, K. Jankowiak-Siuda, I. Szatkowska, Empathy in facial mimicry of fear and disgust: simultaneous EMG-fMRI recordings during observation of static and dynamic facial expressions, *Front. Psychol.* 10 (MAR) (2019) 1–20, <https://doi.org/10.3389/fpsyg.2019.00701>.
- [28] B. Schaal, T.K. Saxton, H. Loos, R. Soussignan, K. Durand, Olfaction scaffolds the developing human from neonate to adolescent and beyond, *Philosophical Transactions of the Royal Society B: Biological Sciences* 375 (1800) (2020), <https://doi.org/10.1098/rstb.2019.0261>.
- [29] L. Schäfer, V.A. Schriever, I. Croy, Human olfactory dysfunction: causes and consequences, *Cell Tissue Res.* 383 (1) (2021) 569–579, <https://doi.org/10.1007/s00441-020-03381-9>.
- [30] A.K. Schobert, C. Corradi-Dell'Acqua, S. Frühholz, W. van der Zwaag, P. Vuilleumier, Functional organization of face processing in the human superior temporal sulcus: a 7T high-resolution fMRI study, *Soc. Cogn. Affect. Neurosci.* 13 (1) (2018) 102–113, <https://doi.org/10.1093/scan/nsx119>.
- [31] R.J. Stevenson, An initial evaluation of the functions of human olfaction, *Chem. Senses* 35 (1) (2009) 3–20, <https://doi.org/10.1093/chemse/bjp083>.
- [32] Thorne, F., Neave, N., Scholey, A., Moss, M., Fink, B., Cognitive, H., Building, N. (2002). Influence of oral contraceptives and the menstrual cycle, 291–297.
- [33] E.M.C. Trecca, M. Cassano, F. Longo, P. Petrone, C. Miani, T. Hummel, M. Gelardi, Results from psychophysical tests of smell and taste during the course of SARS-CoV-2 infection: a review, *Acta Otorhinolaryngologica Italica* 42 (2022) S20–S35, <https://doi.org/10.14639/0392-100X-suppl.1-42-2022-03>.
- [34] W. Zhou, D. Chen, Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions, *Psychol. Sci.* 20 (2) (2009) 177–183, <https://doi.org/10.1111/j.1467-9280.2009.02263.x>.