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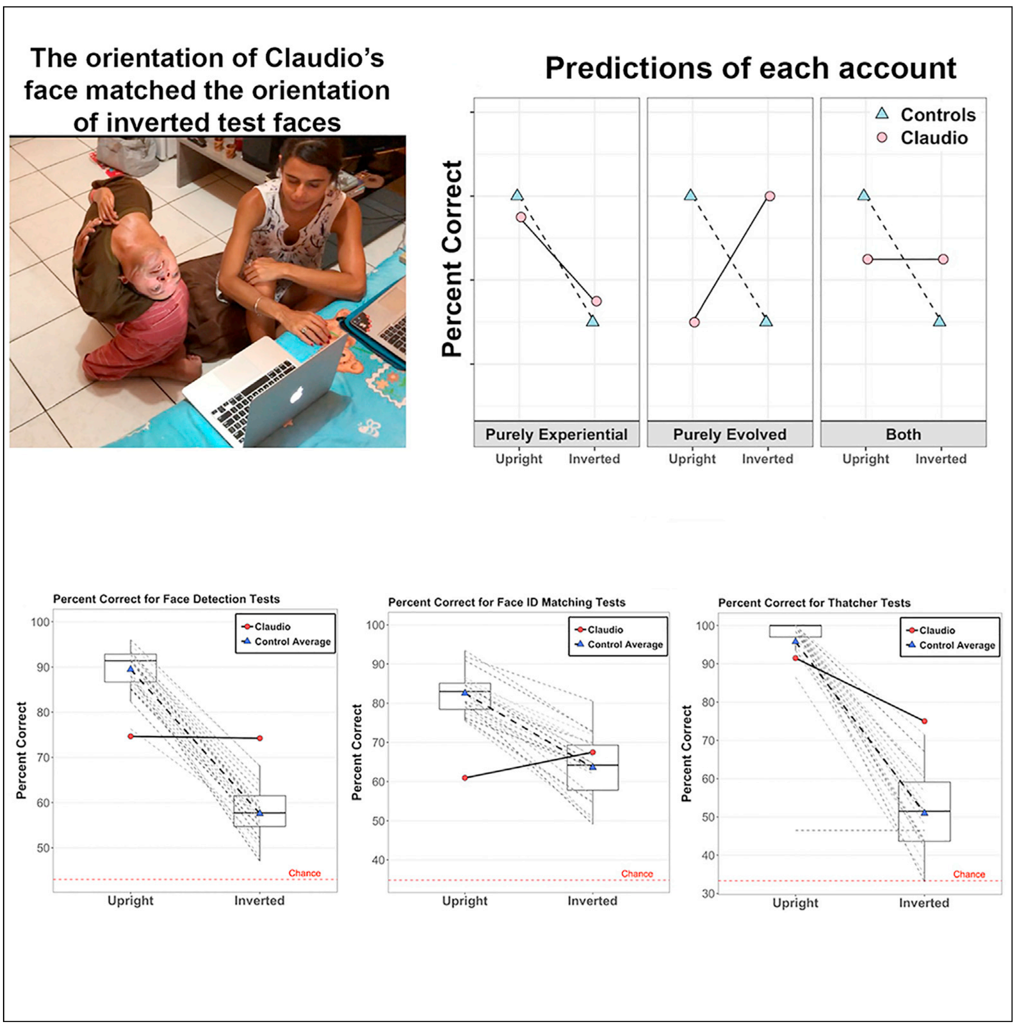

Brad Duchaine, Constantin Rezlescu, Lúcia Garrido, Yiyuan Zhang, Maira V. Braga, Tirta Susilo

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Highlights

Claudio has viewed more faces mismatched to his face's orientation than matched to it

We compared matched vs. mismatched to assess role of experience & evolved factors

No difference for detection, identity matching; mismatched better for Thatcher task

Experience & evolved mechanisms contribute to upright superiority in neurotypicals

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The development of upright face perception depends on evolved orientation-specific mechanisms and experience

Brad Duchaine,[1,6,*] Constantin Rezlescu,[2] Lúcia Garrido,[3] Yiyuan Zhang,[1] Maira V. Braga,[4] and Tirta Susilo[5]

SUMMARY

Here we examine whether our impressive ability to perceive upright faces arises from evolved orientation-specific mechanisms, our extensive experience with upright faces, or both factors. To do so, we tested Claudio, a man with a congenital joint disorder causing his head to be rotated back so that it is positioned between his shoulder blades. As a result, Claudio has seen more faces reversed in orientation to his own face than matched to it. Controls exhibited large inversion effects on all tasks, but Claudio performed similarly with upright and inverted faces in both detection and identity-matching tasks, indicating these abilities are the product of evolved mechanisms and experience. In contrast, he showed clear upright superiority when detecting "Thatcherized" faces (faces with vertically flipped features), suggesting experience plays a greater role in this judgment. Together, these findings indicate that both evolved orientation-specific mechanisms and experience contribute to our proficiency with upright faces.

INTRODUCTION

Adults are highly skilled at perceiving upright faces.[1] Our attention is rapidly drawn to them[2,3], and we can instantly recognize acquaintances and notice subtle changes to facial expressions. Our proficiency with upright faces is especially apparent when the perception of upright faces is contrasted with the perception of inverted faces. When faces are rotated 180° in the picture plane, performance on a wide variety of face processing tasks is substantially reduced[4,5] and in some cases plummets.[6,7] This drop in performance is known as the face inversion effect (FIE), and it is the most fundamental effect in face perception.[8,9]

What are the developmental factors that produce superior performance with upright faces in adults? According to a purely experiential account, the FIE results from the far greater exposure we have to upright faces than inverted faces.[9,10] In contrast, a purely evolved account suggests that superior performance with upright faces results from an evolved orientation-specific component that is tailored for upright faces.[11,12] A third possibility is that the FIE results from both factors.

Previous work has investigated this issue, but the extent to which evolved mechanisms and experience contribute to the development of upright face perception in adults remains unclear. Evidence for evolved mechanisms specialized for upright faces comes from studies demonstrating that newborns attend more to upright faces than inverted faces[13–15] show an inversion effect for facial identity based on the inner features,[16] and exhibit larger frequency-tagged EEG responses over the posterior right hemisphere to upright faces than inverted faces.[17] However, the role these evolved mechanisms play in the development of face processing is difficult to gauge in typical participants because infants spend substantial amounts of time looking at faces,[18,19] most of those faces are upright (i.e., they match the orientation of the infant's face),[20] and the disproportionate experience we have with upright faces persists throughout development. These developmental questions have also been investigated by examining the extent to which laboratory training with inverted faces in adults boosts performance. This approach though has led to mixed results; three studies found little or no effect[21–23] while a study with more extensive training (16 h) produced improvements with inverted faces that reduced the size of the FIE.[24]

The current case study is conceptually similar to the training experiments, but rather than hours of laboratory training with inverted faces, we examine the impact of years of experience with faces mismatched in orientation to an observer's face. Claudio is a 42-year-old man with a congenital joint problem whose head is rotated back almost 180° so that the back of his head sits between his shoulder blades (Figure 1A). As a result, the orientation of Claudio's face, which is upside-down relative to his torso, has usually been reversed in orientation to the faces of other people. Claudio's extraordinary perceptual experience provides an opportunity to test between the three accounts of the FIE discussed above because the experiential and evolved accounts make opposing predictions about Claudio's performance with upright and inverted

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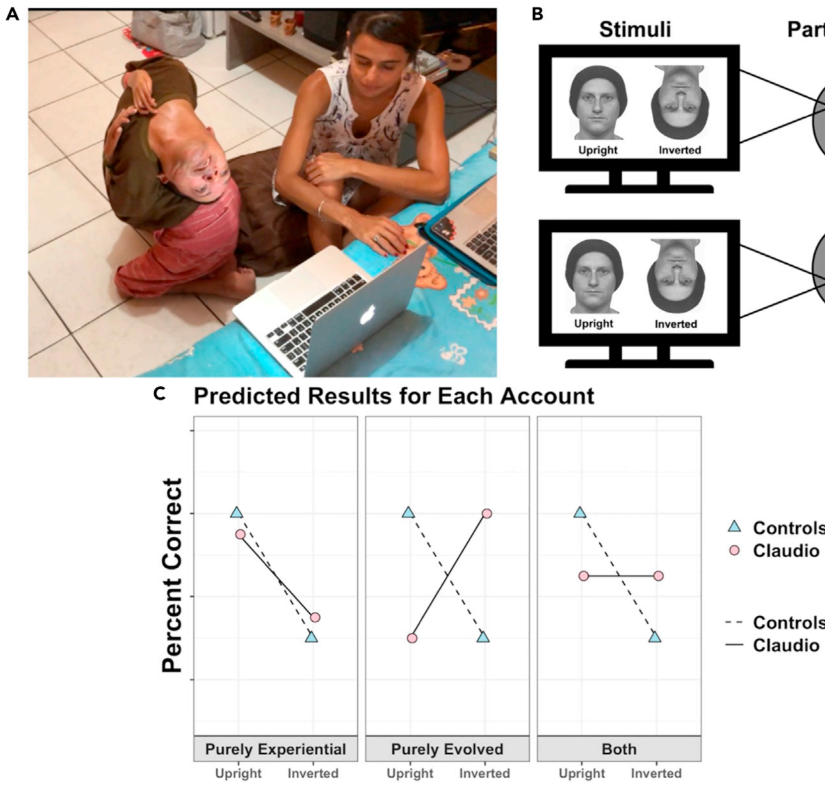

Figure 1. Experimental set-up and the predicted outcomes for each account

(A) For all experiments, Claudio rested on his knees, so the orientation of his face was mismatched to upright faces and matched with inverted faces.

(B) We refer to faces with the eyes above the mouth as *upright* for both Claudio and the controls and faces with the eyes below the mouth as *inverted* for all participants.

(C) A purely experiential account (left panel) suggests that both Claudio and the controls will perform better with upright faces than inverted faces because they have viewed more upright faces than inverted faces. A purely evolved account (middle panel) predicts both Claudio and the controls will perform better with the face orientation that matches the orientation of their face than the opposite orientation. If both evolved factors and experience contribute to upright superiority in typical individuals (right panel), then Claudio's performance will be somewhere in between the predictions of the purely evolved account and the purely experience account. In our example plot for Both, controls have a typical FIE while Claudio's performance with upright and inverted faces is comparable.

faces (Figures 1B and 1C). Because Claudio has had more experience with upright faces than inverted faces, the experiential account predicts Claudio will perform better with upright faces than inverted faces. In contrast, the evolved account predicts Claudio will show superior performance with inverted faces because inverted faces match the orientation of his face. If experience and evolved factors both contribute to the FIE, Claudio should exhibit roughly comparable performance with upright and inverted faces. Claudio's relative performance with upright and inverted faces may differ for distinct face tasks because different aspects of face processing depend on separable processes[1,25] and these separable processes may have different developmental trajectories.[26,27]

RESULTS

Claudio's case description

Claudio was born with arthrogryposis multiplex congenita, a condition in which the range of motion of multiple joints is restricted. In Claudio's case, joints in his legs, arms, and neck are in permanently fixed positions. When Claudio was born, physicians told his parents that there was nothing that could be done for him and that he would not survive. However, Claudio's parents believed they could support him, and despite great challenges, Claudio has led an inspiring life. He began walking on his knees at the age of eight. His mother taught him to read, he writes by holding a pen in his mouth, and he uses a pointer in his mouth to type. He attended school and then obtained a degree in accounting at a university 4 h from his hometown. He works as a tax accountant, gives motivational speeches, wrote an autobiography, and has a large social media following. Claudio has an engaging personality and greeted us enthusiastically each morning we arrived at his home for testing sessions.

Claudio tends to rest on his knees when interacting with others so that the orientation of the faces he views are mismatched to his face's orientation (Figure 1A). He also kneels when watching television so his face and faces on television are mismatched. Claudio sometimes lies on his side, where the orientation of his face differs by around 90° from the faces he views. He also told us that he has occasionally spent time lying on the front of his torso with his head tilted up and then the orientation of his face matches the orientation of faces around him. Claudio's mother reports that she cradled him as an infant with the front of his torso facing down and his shoulders close to her upper arm. That allowed them to be face-to-face, but the orientation of their faces was mismatched. She also carried Claudio with his body upright and the front of his torso resting against her body which again left his face's orientation mismatched to faces around him. Our understanding of Claudio's positioning during his life as well as observations of it during our time with him have led us to conclude that he has had much more experience with faces that are mismatched in orientation to his own face than those that are matched. Later in discussion we also report data that provides empirical support for this conclusion.

Testing Claudio's face processing abilities

We tested Claudio in 2015 and 2019. In 2015, we ran tasks assessing face detection and facial identity matching. In 2019, we again used detection and identity-matching tasks and added tasks requiring the detection of Thatcherized faces. The tasks were chosen because they generate large inversion effects in controls. Our report focuses on the 2019 testing because we tested Claudio with more tests in 2019 and those tests produced larger inversion effects in controls than the 2015 tests. The 2015 data were quite similar to the 2019 data, and it is included in the Supplementary Information (Figure S4; Table S1).

Throughout this article, we label faces *upright* when the eyes are above the mouth and *inverted* when the eyes are below the mouth (Figure 1B). Therefore, upright and inverted faces for Claudio and the controls are identical, and our labels are not influenced by the orientation of the participants' faces. In all the testing with Claudio, he kneeled in front of the laptop which meant that his face's orientation was *mismatched* to upright faces and *matched* with inverted faces (Figure 1A, Video S1). Controls made keypress responses for most tasks whereas Claudio responded verbally and then his response was recorded via a keypress by an experimenter. As a result, Claudio's response times on keypress tasks include the time the experimenter took to respond. This issue is not present in the three detection tasks, one identity matching task, and one Thatcher task in which vocal responses were recorded so Claudio's response times on those tasks can be better compared to the controls' response times. Claudio's performance was compared to 22 age-matched control participants for the face detection, face identity matching, and Thatcher tasks discussed later in discussion (STAR methods).

Face detection: Large inversion effect for controls and no inversion effect for Claudio

Detection of the presence of a face in a visual display is a critical step in both primate and machine face processing.[28,29] We used seven face detection tasks to assess upright and inverted face detection. The detection tasks required participants to detect the presence of a face in either two-tone images (e.g., Mooney faces) or arrays of two-tone face parts (Figure 2A; STAR methods). Because of the noise present in results for individual participants in any single task, we focus on average accuracy and response times for upright and inverted faces across the seven tasks. These averages were calculated by weighting each task based on the number of trials (for details about each task, see Table in STAR methods). The results for each task are displayed in Figure S1, and the statistical results for individual tasks are listed in Table S2.

Figure 2B shows that each control showed far better detection of upright faces (M = 89.5%, SD = 4.7%) than inverted faces (M = 57.6%, SD = 5.9%), demonstrating the classic face inversion effect (FIE), here defined as upright accuracy *minus* inverted accuracy (mean FIE = 31.9%, SD = 4.8%; range = 21.1%–41.1%). The FIEs were significantly greater than zero as shown by a one-sample t-test ($t(21) = 16.10$, $p < 0.001$). The controls' FIE was also apparent in response times, which is defined here as inverted response time *minus* upright response time (mean RT FIE = 1340.4 ms, SD = 742.8 ms) and this effect was also significantly greater than zero ($t(21) = 10.13$, $p < 0.001$) (Figure 2C). In contrast, Claudio showed almost identical accuracy for upright (74.7%) and inverted (74.3%) faces, and his FIE (0.4%) was significantly smaller than the controls' FIE as demonstrated by a modified t-test for single case comparisons ($t(21) = -3.75$, $p = 0.001$). Claudio's response times for upright and inverted faces were also similar (Figure 2C), though his response time FIE (−183.5 ms) was not significantly smaller than the controls' FIE ($t(21) = -1.84$, $p = 0.078$). Overall, Claudio's comparable performance with upright and inverted faces is consistent with both experiential factors and evolved factors contributing to upright face detection in typical participants (Figure 1C).

The predictions made by the developmental accounts discussed above are concerned with Claudio's relative performance with upright and inverted faces (Figure 1C). However, it is also informative to examine Claudio's performance with upright and inverted faces separately. Figure 2B shows that Claudio's accuracy with both upright and inverted faces is far above chance level (43.0%). Thus, the absence of an FIE in Claudio's accuracy results is not due to restrictions of range for either orientation. Claudio's upright accuracy is significantly worse than the controls' upright accuracy ($t(21) = -3.11$, $p = 0.005$), while his inverted accuracy is significantly superior to the inverted accuracy of the controls ($t(21) = 2.77$, $p = 0.011$) (Figure 2B). Claudio's upright response times were also significantly slower than controls' ($t(21) = 4.41$, $p < 0.001$) (Figure 2C), but his inverted response time was in the middle of the distribution of the control response times ($t(21) = -0.52$, $p = 0.611$). These comparisons demonstrate that Claudio's comparable performance with upright and inverted faces resulted from impaired upright detection and superior inverted detection.

It is also worthwhile to compare performance with faces in the mismatched orientation, which is upright for Claudio and inverted for controls. That comparison may support inferences about the effect of experience on the perception of mismatched faces because Claudio has had more experience with upright faces than controls have had with inverted faces. For face detection, Claudio's upright accuracy (74.7%) is superior to the inverted accuracy of every control (M = 57.6%, SD = 5.9%), and the difference is significant ($t(21) = 2.84$, $p = 0.010$). Claudio's upright response time (2492.7 ms) and the controls' inverted response times (M = 2740.1 ms, SD = 817.1 ms) were similar ($t(21) = -0.30$, $p = 0.770$). These findings indicate that experience with mismatched faces does improve detection of them.[24]

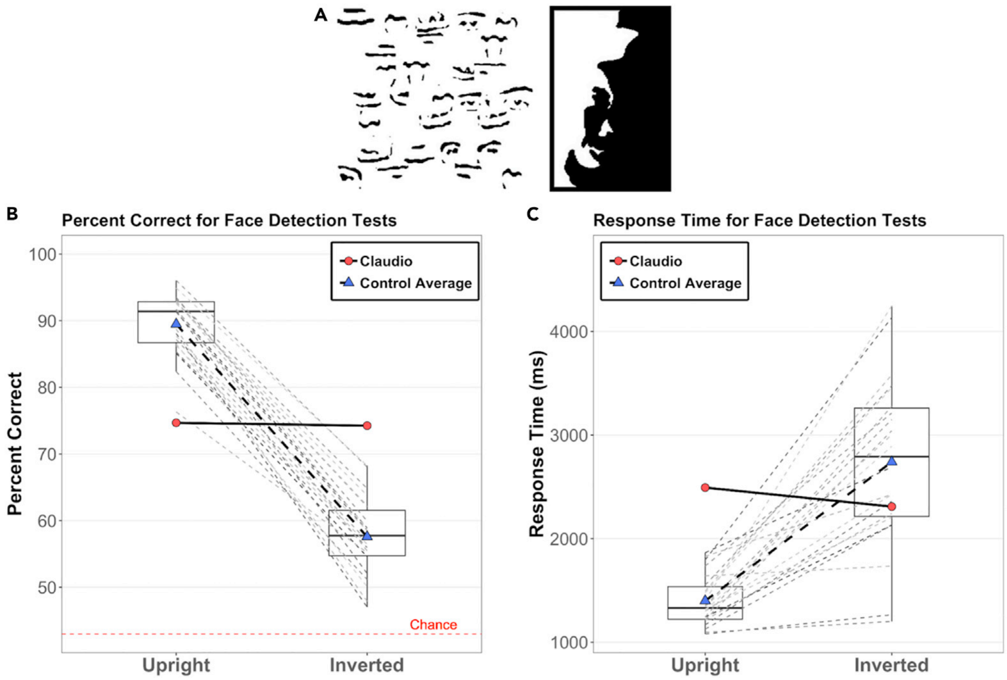

Figure 2. Stimuli and results for face detection tests

(A) Two types of stimuli were used in the seven face detection tasks. Both are shown inverted; rotate the page to view them upright. Face part array stimuli consisted of a collection of face parts drawn from thresholded images of faces (left). The array on the left side of Panel A includes a region in which the face parts formed a face. Other tasks used Mooney faces like the face shown on the right[58,59].

(B) Claudio's average accuracy across the seven face detection tasks is displayed with red circles. Mean control accuracy is shown with blue triangles, and accuracy for individual controls is represented by the ends of the faint dashed lines. The dark line in the box displays the control median, the bottom and top of the box show the 25th and 75th percentiles, and the whiskers show 1.5 * the interquartile range.

(C) Average response times for Claudio and the controls using the same conventions as Panel B.

The results for individual face detection tests (Figure S1; Table S1) show that controls consistently exhibited face inversion effects whereas Claudio was better with upright faces in some tests, better with inverted faces in other tests, and showed little difference in the remaining tests. These varied inversion effects for Claudio could indicate that different detection tasks measure different processes. Alternatively, the swings could reflect normal FIE variability for a participant whose true FIE for detection and identity matching is close to zero. To test between these possibilities, we compared the variation in the size of Claudio's FIEs and the controls' FIEs. In this analysis, we calculated the standard deviation of the FIE for each control and for Claudio on the seven face detection tasks. The results demonstrated that the standard deviation of Claudio's detection FIEs is slightly less than the control average, and Claudio's standard deviation is not significantly different from the control standard deviation (Detection: $t(21) = -0.54$, $p = 0.590$) (Figure S5). Thus, the swings from upright superiority to inversion superiority in Claudio's detection results are what would be expected for a participant whose true FIE is around zero.

Face identity matching: Large inversion effect for controls and no inversion effect for Claudio

Face identity discrimination is a core function of the human face processing system.[30,31] Claudio's performance with upright and inverted face identity perception was measured with seven tasks that required either identity matching across different views (Figure 3A) or a same/different identity judgment about two faces shown in different viewpoints. Average accuracy and response times were again calculated by weighting each task based on the number of trials. The results for each of the seven tasks are displayed in Figure S2 and Table S2.

As expected, the controls' accuracy was much better for upright faces ($M = 82.5\%$, $SD = 5.2\%$) than inverted faces ($M = 63.6\%$, $SD = 8.2\%$), with a mean FIE of 18.9% ($SD = 5.9\%$) and a range from 10.6% to 33.5% (Figure 3B). The FIE was significantly above zero for controls ($t(21) = 14.95$, $p < 0.001$). In contrast, Claudio was slightly more accurate with inverted faces (67.5%) than upright faces (61.0%), and Claudio's FIE (−6.6%) was significantly smaller than the controls' FIE, ($t(21) = -3.11$, $p = 0.005$). The controls' FIE was also apparent in their response times ($M = 367.9$ ms, $SD = 268.4$ ms, $t(21) = 10.13$, $p < 0.001$) (Figure 3C). Claudio responded more quickly on trials with upright faces (4002.8 ms) than inverted (4181.9 ms) but Claudio's response time FIE (−179.2 ms) was not significantly different from controls' FIE ($t(21) = -0.68$, $p = 0.501$). Overall, the results for identity matching lead to similar conclusions as the face detection results. Because Claudio has had more experience with upright than inverted faces, his roughly comparable performance with upright and inverted faces indicates that both experiential factors and evolved factors contribute to the development of facial identity perception in typical participants.

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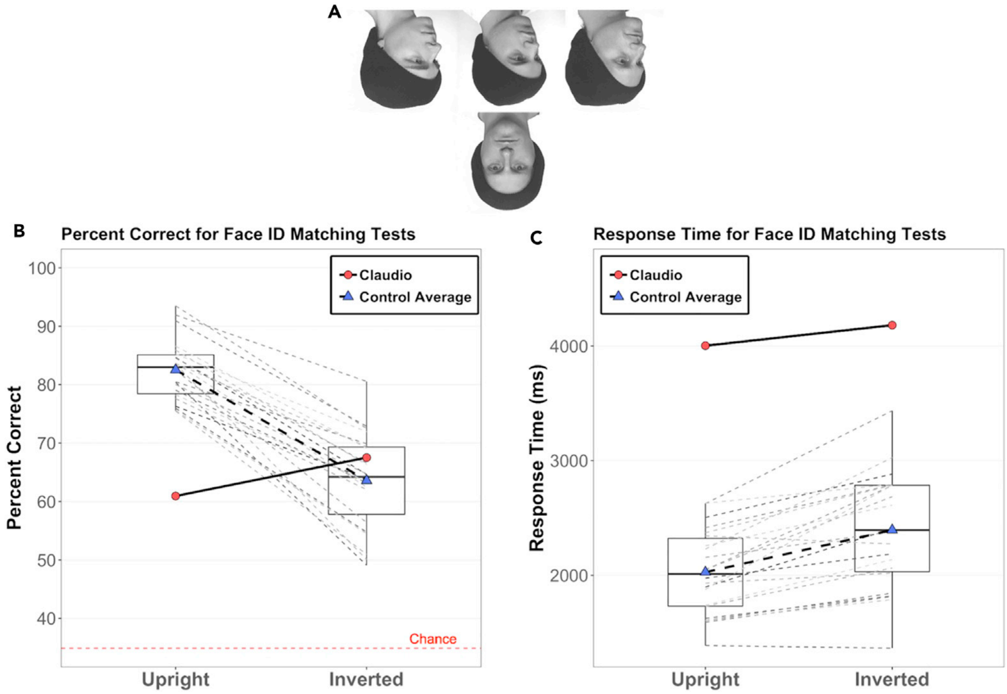

Figure 3. Stimuli and results for face identity-matching tasks

(A) A variety of stimuli were used in the face identity-matching tasks. Five of the seven tasks were three-alternative forced-choice paradigms similar to the inverted example shown here. A target stimulus was briefly presented. After the target was removed from the screen, three test faces were displayed. Two faces were distractors and the third face was the target identity. The viewpoint of the distractors always differed from the viewpoint of the target.

(B) Claudio's average accuracy across the seven face identity-matching tasks is displayed with red circles. Mean control accuracy is shown with blue triangles, and accuracy for individual controls is represented by the ends of the faint dashed lines. The box displays the median, 25th percentile, and 75th percentile while the whiskers indicate 1.5 * the interquartile range.

(C) Response times for Claudio and the controls are displayed using the same conventions.

Accuracy for Claudio and the controls on the identity-matching tasks was well above chance level (36.0%) (Figure 3B), so restrictions of range do not explain Claudio's comparable performance with upright and inverted faces. Claudio's upright accuracy was significantly worse than the controls' upright accuracy ($t(21) = -4.03$, $p < 0.001$), but his inverted accuracy was in the midst of the controls' inverted accuracy distribution ($t(21) = 0.47$, p =0 .646) (Figure 3B). Thus, Claudio's comparable performance with upright and inverted faces was driven by performance with upright faces that is reduced relative to control performance. For the mismatched comparison, Claudio's accuracy with upright faces (61.0%) was similar to the controls' accuracy with inverted faces ($M = 63.6\%$, $SD = 8.2\%$, $t(21) = -0.31$, $p = 0.756$), so this comparison does not provide evidence that experience with mismatched faces improves identity matching performance with them.

Detection of Thatcherized faces: Large inversion effect for controls and moderate inversion effect for Claudio

Our third set of tasks required participants to detect "Thatcherized" faces. When facial features are inverted within a face (e.g., eyes and mouth rotated 180°), upright faces appear grotesque but the change is challenging to notice in inverted faces.[32] In this task, participants attempted to identify a Thatcherized face from three simultaneously presented faces, two of which were unmanipulated and one which had been Thatcherized by inverting the eyes, the mouth, or both (Figure 4A). Each participant was tested twice with the task, once with keypress responses and once with vocal responses (Figure S3; Table S2 for results for each administration).

Accuracy and response times were averaged across the two administrations of the task; Claudio's results for each administration were nearly identical (Figure S3). Average upright accuracy for controls was 95.8% (SD = 11.5%) while inverted accuracy was 51.0% (SD = 10.0%), thus controls showed extremely large FIEs on the Thatcher tasks ($M = 44.8\%$, $SD = 13.5\%$, $t(21) = 14.11$, $p < 0.001$) (Figure 4B). Claudio performed much better with upright faces (91.5%) than inverted faces (75.0%), and his FIE (16.5%) was numerically smaller but not significantly different than the controls' FIE ($t(21) = -1.88$, $p = 0.07$) (Figure 4B). The controls' response time for inverted faces ($M = 2794.4$ ms, $SD = 709.1$ ms) was much slower than their response times for upright faces ($M = 1400.9$ ms, $SD = 381.2$ ms) (Figure 4C), with a mean FIE of 1393.5 ms ($SD = 821.9$ ms), which was significantly above zero ($t(21) = 7.21$, $p < 0.001$). Claudio's FIE (−134.5 ms) was smaller than the controls' FIE but this difference was not significant ($t(21) = -1.70$, $p = 0.103$).

Figure 4B shows that Claudio's accuracy with upright faces was within the normal range of the controls' upright accuracy ($t(21) = -0.36$, $p = 0.720$) whereas Claudio's inverted accuracy was superior to the inverted accuracy of the controls ($t(21) = 2.35$, $p = 0.029$). Thus, Claudio's FIE

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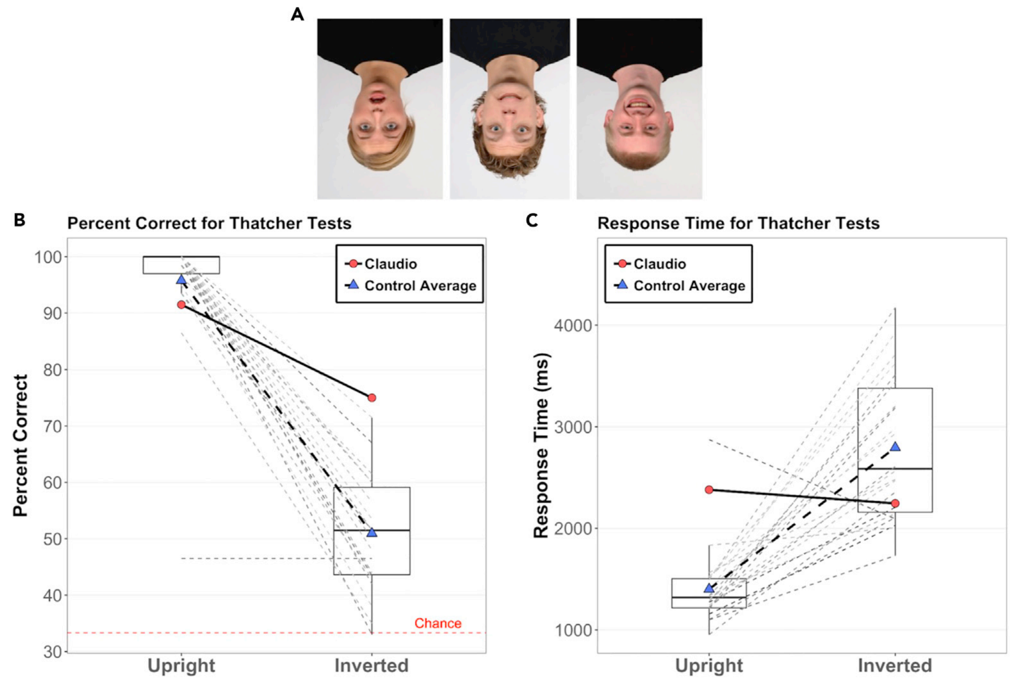

Figure 4. Stimuli and results for Thatcher tasks

(A) Faces from a trial in the Thatcher task are shown inverted. Participants attempted to choose the face that looked strange. In this example, the eyes and mouth of one of the faces were rotated 180° within the face (rotate the figure to see the Thatcherized face).

(B) Claudio's average accuracy across the two Thatcher tasks is displayed with red circles. Mean control accuracy is shown with blue triangles while individual data points are displayed with faint dashed lines. The box displays the median, 25th percentile, and 75th percentile while the whiskers indicate 1.5 * the interquartile range.

(C) Response times for Claudio and the controls are displayed using the same conventions.

was smaller than the controls' FIE primarily because his accuracy with inverted faces was unusually high. Turning to mismatched faces, Claudio's upright accuracy was superior to the inverted accuracy of every control ($t(21) = 3.96$, $p < 0.001$). Response times for Claudio with upright faces and controls with inverted faces were comparable ($t(21) = -0.57$, $p = 0.573$). This comparison of performance with mismatched orientations indicates that experience with mismatched faces boosts the detection of Thatcherized faces.

Comparisons between Claudio's performance on the three types of tasks

The results above tested whether Claudio's performance differed from the performance of the control participants on each type of task separately. Next, we compare if the differences in Claudio's performance between each pair of the three types of tasks was significantly different than the differences observed in controls for the same pair of tasks. These differences were tested using the Revised Standardized Difference Test (RSDT)[33] with Bonferroni correction for three pairs of comparisons (corrected alpha = 0.0167). In addition to the results later in discussion, we also compared Claudio's inverted accuracy to the controls' inverted accuracy and Claudio's inverted accuracy to the controls' upright accuracy (Table S3).

We first compared the FIEs across tasks. The difference between Claudio's FIE for face detection and his FIE for face identity matching was not significantly different from the differences in controls ($t(21) = 1.91$, $p = 0.07$). The differences between Claudio's face identity matching and Thatcher detection FIEs were also not significantly different from the controls' differences ($t(21) = 1.38$, $p = 0.183$). However, the contrast between face detection and Thatcher detection was significant ($t(21) = 2.67$, $p = 0.014$), because controls showed large FIEs for both types of tasks whereas Claudio had a substantial FIE for Thatcher detection but no FIE for face detection. This finding indicates that the mechanisms supporting Thatcher processing are more sensitive to the influence of experience than those involved with face detection.

We next compared differences in upright accuracy across tasks. Claudio's difference between upright accuracy for Thatcher detection and face identity matching was significantly larger than the differences observed in controls ($t(21) = 2.83$ $p = 0.010$). Like the FIE difference found above, this difference suggests that performance with upright Thatcher detection is more strongly influenced by experience than another task, which in this case is face identity matching. The two other comparisons were not significant (Thatcher detection versus face detection ($t(21) = 2.17$, $p = 0.042$); face detection versus face identity matching ($t(21) = 0.85$, $p = 0.404$)).

We then compared differences in Claudio's upright accuracy against differences in controls' inverted accuracy across tasks. This comparison allows us to directly test whether experience with faces in mismatched orientation improved accuracy with some tasks more than others.

Claudio's difference for the upright Thatcher detection and the upright face identity-matching tasks was significantly larger than the differences of the controls in the inverted conditions of these tasks ($t(21) = 3.35$, $p = 0.003$). Similarly, Claudio's difference for upright face detection and upright face identity matching was also significantly larger than the controls' difference for the inverted conditions for these tasks ($t(21) = 3.19$, $p = 0.004$). No difference for face detection versus Thatcher detection was observed ($t(21) = 0.89$, $p = 0.385$). Overall, this analysis suggests that experience with mismatched faces facilitates performance on face detection and Thatcher detection to a similar degree, more than it does for face identity matching.

DISCUSSION

We tested the predictions of three accounts of the factors that lead to our outstanding abilities with upright faces and which produce the face inversion effect (Figure 1C). Controls exhibited inversion effects that were substantial for all tasks, and inversion effects for several tasks were some of the largest in the literature.[4,34] These robust inversion effects allowed us to determine which of the predictions matched the relationship found for Claudio's upright and inverted performance.

The results for face detection and face identity matching were similar so we will discuss them together. Claudio showed nearly identical accuracy for upright and inverted face detection along with comparable response times. For identity matching, Claudio was slightly more accurate with inverted faces than upright faces and produced comparable response times for upright and inverted faces. The similarity of Claudio's performance with upright and inverted faces for both detection and identity matching is consistent with the mixed account that involves both evolved and experiential factors. Thus, Claudio's results indicate that the development of upright face detection and face identity matching in typical individuals reflects both the tuning that occurs due to massive exposure to upright faces and the operation of orientation-specific mechanisms that have evolved to process upright faces.

The evolved mechanisms supporting upright face detection and identity matching in adults may be mature versions of the mechanisms that operate at birth,[13,16,17,35] other evolved face processes that emerge after birth, or a combination of the two. Support for the first possibility comes from studies suggesting that the mechanisms that direct attention to faces in infants continue to play a role in face perception in children[36] and adults.[37,38] Our findings pointing to the operation of evolved mechanisms in adults are also consistent with demonstrations of face-selective activation on the lateral fusiform gyrus in response to auditory and tactile presentations of faces in participants who are congenitally blind and who therefore have had no visual experience with faces.[39,40]

Experience with visual stimuli in particular orientations produces gains in performance at the practiced orientations on many tasks[41–43] so our expectation was that Claudio's results would show that experience plays a role in our sensitivity to upright faces. Two types of comparisons involving Claudio's results provided support for the effect of experience. First, Claudio's upright performance relative to his inverted performance in all three types of tasks was clearly inconsistent with the purely evolved predictions so his results indicate that experience improves the perception of faces matched in orientation to an observer's face. While this conclusion is not surprising given previous results with other visual judgments as well as demonstrations that face training at particular viewpoints selectively improves performance,[44,45] it is the only evidence we are aware of that directly indicates that experience contributes to the development of our sensitivity to upright faces. Second, Claudio's accuracy with upright face detection and upright Thatcher tasks was superior to the controls' inverted accuracy for these tasks. Because Claudio has had more experience than controls with faces in a mismatched orientation, this difference provides evidence for an effect of experience on mismatched face perception similar to what was found when participants trained with inverted faces for 16 h.[24]

The results from the Thatcher tasks suggest a qualitatively different pattern than that found for the detection and identity-matching tasks. On the Thatcher tasks, Claudio achieved normal accuracy with upright faces and performed better with upright faces than inverted faces. In contrast, Claudio's upright face detection and identity matching performance was clearly worse than the controls' performance, and he showed little difference between his upright and inverted performance. While we interpret these differences between the different types of tasks cautiously because the Thatcher findings are based on a single task format and not all comparisons of differences between tasks were significant, they suggest that upright performance on Thatcher tasks is more dependent on experience than upright detection and identity matching. Our results do not speak to why this difference occurs, but we note that the ability to detect upright faces and to recognize facial identity in upright faces were likely selected for in ancestral environments whereas the identification of Thatcherized faces is not a natural task. Thus, detection and identity matching may depend on processes that were evolutionarily generated to address these ancestral challenges whereas Thatcher detection may be more akin to visual problem solving[46] and so may be less dependent on evolved face processes.

Claudio's better performance with upright faces than inverted faces in the Thatcher tasks also provides empirical evidence that bolsters our inferences about the factors influencing detection and identity matching. Based on our observations of Claudio during testing visits with him, his self-report about his positioning in daily life, and his mother's recollections of his positioning during infancy, we felt confident that Claudio has had considerably more experience with mismatched (i.e., upright) faces than matched (i.e., inverted) faces. However, our inference from that information could be mistaken and left open the possibility that Claudio had comparable amounts of experience with faces matched and faces mismatched to his face's orientation. If that scenario was correct, Claudio's comparable upright and inverted detection and identity matching could be accounted for by the purely experiential account and his results would not implicate an evolved factor in the development of face perception. However, Claudio's accuracy with upright faces on the Thatcher tasks was 16.7% better than his accuracy with inverted faces. This difference was identical across the two administrations of the task and did not result from speed/accuracy tradeoffs. Because a consistent upright advantage in Claudio can only be accounted for by greater experience with upright faces than inverted faces, this result indicates Claudio has had more experience with upright faces than inverted faces and therefore reinforces our conclusion that the development of upright face detection and upright identity matching involve both experience and evolved factors.

Psychologists and neuroscientists have had a long-running interest in the role that evolved mechanisms and experience have on our psychological abilities and traits. In most cases though, experience cannot be manipulated for ethical or practical reasons, and when it can be manipulated, it can only be done for a short period of time. Claudio's case is extraordinary in that it provides an opportunity to examine the effect of a lifetime of seeing the visual world from a different perspective. The results of the study indicate that our extensive experience with upright faces as well as evolved orientation-specific procedures combine to make upright face detection and upright identity matching so much better than inverted detection and matching. In addition, Claudio's contrasting results for face detection and matching compared to Thatcher detection suggest that different face processing functions are developmentally dissociable, a finding consistent with the dissociations found in neurotypical participants[27] and in developmental prosopagnosia.[6,26,47] Our study used three types of face tasks, but the effects of orientation are ubiquitous in face perception[48–50] and are also present for other aspects of visual perception[51,52] so we expect further investigation of Claudio's visual processing is likely to be revealing.

Limitations of the study

Many of the inferences drawn from Claudio's results are dependent on our conclusion that he has had considerably more experience with faces that are reversed in orientation to his own face than with faces that match his face's orientation. However, no objective record of Claudio's previous experiences with upright and inverted faces exists. In the future, we would like to collect video from a head-mounted camera that would record the orientation of the faces Claudio views,[53] but it will never be possible to precisely quantify his past experiences with faces. Nevertheless, our discussions with Claudio and his mother as well as our observation of Claudio's everyday interactions with others make us confident that he has had more experience with upright faces than inverted faces and indicate that that was true early in life as well. In addition, clear empirical support for this conclusion is provided by his consistent upright superiority in the Thatcher judgments.

Our interpretation of Claudio's results assumes that his performance on the face-processing tasks relies on the perceptual mechanisms that support face perception in typical participants. However, Claudio's unusual experience with faces may have interacted with his developing visual system such that the faces he views today do not engage the network of face-selective areas that face processing depends on in typical participants.[1,25] For example, it is possible that an evolved face processing system in the infant atrophies in the absence of a steady volume of faces in a manner similar to the effects of monocular deprivation on ocular dominance maps in early visual cortex.[54] If this occurred, then Claudio may have completed the tasks or some of the tasks using alternative mechanisms and his results may tell us little about the relative contributions of evolved mechanisms and experience to our upright face perception abilities. Examination of Claudio's response to faces and other categories with fMRI is probably not feasible, but EEG[55,56] and near-infrared spectroscopy[57] may provide a means to determine whether his perception of faces relies on mechanisms comparable to those in typical visual systems.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2023.107763.

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AUTHOR CONTRIBUTIONS

B.D. designed the study, tested Claudio in 2019, contributed to testing the 2015 and 2019 controls, and wrote the article. C.R. and L.G. designed the study, tested Claudio in 2015, and wrote the article. Y.Z. tested the 2019 controls, analyzed the data, created the figures, and wrote the article. M.B. tested Claudio in 2019. T.S. designed the study, tested 2015 controls, and wrote the article. All authors approved the final version of the article.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Experimental data	This paper	Database: https://figshare.com/projects/The_Development_of_Upright_Face_Perception_Depends_on_Evolved_Orientation-Specific_Mechanisms_and_Experience/150507
Software and algorithms		
Analysis scripts	This paper	Database: https://figshare.com/projects/The_Development_of_Upright_Face_Perception_Depends_on_Evolved_Orientation-Specific_Mechanisms_and_Experience/150507

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Brad Duchaine (bradley.c.duchaine@dartmouth.edu).

Materials availability

This study did not generate reagents.

Data and code availability

- The datasets from the current study have been deposited in a public repository. Database: https://figshare.com/projects/The_Development_of_Upright_Face_Perception_Depends_on_Evolved_Orientation-Specific_Mechanisms_and_Experience/150507.
- All statistical analyses were run in R 4.0.567 using code that implement the algorithms described in the papers that introduced these statistical tests33,65. All scripts are available online at figshare.
- The lead contact will provide any additional information needed to reanalyze the data reported in the paper.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Participants

Claudio was 42 years old when the 2019 data reported here was collected. Testing was conducted in Claudio's home over a three-day period. Claudio kneeled in front of a laptop placed at his eye level (Figure 1A; Video S1). Author M.B. sat next to Claudio so she could start each experiment, explain the instructions to Claudio in Portuguese, and make keypresses to record Claudio's verbal responses.

Claudio was also tested in his home by authors L.G. and C.R. over a three-day period in 2015. That testing included several of the face detection and face identity-matching tests used in 2019, and the results from the detection and identity-matching tasks run in 2015 are displayed in Figure S4. The 2015 results were comparable to what we found in the 2019 testing. Controls showed substantial face inversion effects, whereas Claudio's average performance with upright and inverted faces across the five detection tasks and the five identity-matching tasks was nearly identical. After the 2015 testing, we decided to carry out more testing with Claudio after removing tasks that generated small inversion effects in controls, adding tests with large inversion effects, converting several tests from keypress responses to microphone responses, and creating the Thatcher tasks.

As background data, Claudio's performance on standard face recognition tasks was measured. We created a 56-item famous face test suitable for Brazilian participants and tested Claudio, his 41-year-old sister, and a 59-year-old female neighbor. Each famous face was presented upright for 3 s. Claudio correctly identified 19 of the faces whereas his sister and neighbor identified 26 and 36 faces, respectively. After the test, we asked all three participants about their exposure to the celebrities, and they reported comparable exposure (Claudio = 49/56; Sister = 50/56; Neighbor = 50/56). We tested Claudio's short-term memory for upright unfamiliar faces with the Cambridge Face Memory Test.[60] His score of 45.8% (or 33 out of 72) is well outside the normal range for US participants (mean = 84.0%, sd = 11.0%).

We also measured Claudio's low-level and mid-level visual abilities. On four subtests from the Birmingham Object Battery Test,[61] Claudio scored 24 on the length match task, 27 on the size match task, 21 on the orientation match task, and 34 on the position of gap match task. On the Leuven Perceptual Organization Screening Test,[62] Claudio scored 5/5 on 3 subtests and 4/5 on the remaining 12 subtests.

Controls

Claudio's 2019 performance was compared to 22 age-matched control participants (14 men, 8 women). The average age of the controls was 39.41 (SD = 3.70). All were recruited through Testable Minds and were tested remotely using Testable.[63] Controls were tested in three sessions. Controls and Claudio did the tests in the same order.

Eight control participants (4 men, 4 women; average age = 22.75 (SD = 1.49) were tested with the set of tasks run with Claudio in 2015. They were tested in person and did the tests in the same order as Claudio.

The study adhered to the Declaration of Helsinki and was approved by Dartmouth's Committee for the Protection of Human Subjects. Both Claudio and the controls provided informed consent.

METHOD DETAILS

Face perception tasks

Participants were tested with 16 tasks. Claudio was tested over three days, and controls were tested in three sessions conducted on different days. Face detection, identity matching, and Thatcher tasks were interleaved, and the position of each task in the full set of tasks is displayed in table below.

Face detection

On trials in the face detection tests, a single image or set of images was presented. For the single images, participants were asked to judge if there was a face in the image; a face was present in half the images. For the sets of images, participants were instructed to select the one image that contained a face. Stimuli were Mooney faces[58,59] or clusters of two-tone face parts that either created a coherent face or did not[6] (Figure 2A). Table provides details about each task. Each image or set of images was presented upright once and inverted once, with the image shown upright first half of the time. Within each task, sets of upright and inverted faces were presented in blocks, and participants were informed at the start of each block whether the images would contain upright or inverted faces. Participants were provided with practice trials at the start of each task.

Details for face detection tasks

Face Detection

Task	Presentation of Stimuli	Stimulus Duration (ms)	Decision	Response	# of Trials	Up/Inv Presentation	Task position	Chance Accuracy (%)	Randomization
Two-Tone 2AFC 600ms	Simultaneous	700	Forced Choice	Keypress	120	Interleaved Blocks	1	50	Yes - Within Block
Mooney 3AFC	Simultaneous	500	Forced Choice	Keypress	78	Interleaved Blocks	3	33	Yes - Within Block
Two-Tone 3AFC	Simultaneous	Until Response	Forced Choice	Keypress	90	Interleaved Blocks	6	33	Set Order
New Mooney 3AFC Voice	Simultaneous	2000	Forced Choice	Voice	180	Interleaved Blocks	9	33	Yes - Within Block
Two-Tone 2AFC 3s Voice	Simultaneous	3000	Forced Choice	Voice	120	Interleaved Blocks	10	50	Yes - Within Block
Mooney Yes-No	Simultaneous	600	Face/No Face	Keypress	120	Interleaved Blocks	11	50	Yes - Within Block
Two-Tone Yes-No	Simultaneous	2000	Face/No Face	Voice	120	Interleaved Blocks	14	50	Yes - Within Block

All stimuli on a trial were displayed simultaneously. Trials were organized in blocks consisting of either ten trials with upright stimuli or ten trials with inverted stimuli. Prior to each block, participants were told whether a block involved upright faces or inverted faces. Task position refers to the position of the task among all the tasks run with Claudio and the controls. The order of the trials within a block was randomized for all tasks except for Two-Tone 3AFC.

Facial identity matching

In six of the seven identity-matching tasks, a target face was briefly presented, followed by the presentation of three test faces (Figure 3A). Participants were asked to choose the face that matched the target face or, in the case of the Dartmouth Face Perception test, was most similar to the target face. For the Identity Same/Different task, two faces were presented sequentially, and participants reported if their identities were the same or different. The viewpoint of the target face and the test faces always differed. Each trial was presented upright and inverted, with each trial presented upright first half of the time. In table, additional information is provided about each task.

Details for facial identity matching tasks

Facial Identity Matching

Task	Target/ Probe Presentation	Target Duration (ms)	Probe Duration (ms)	Decision	Response	# of Trials	Up/Inv Presentation	Task position	Chance Accuracy (%)	Randomization
Dartmouth Face Perception Test	Simultaneous	Until Response	Not Applicable	Forced Choice	Keypress	80	Interleaved Blocks	2	33	Yes - Within Block
Harvard ID 3AFC	Sequential	800	4000	Forced Choice	Keypress	80	Interleaved Blocks	5	33	Yes - Within Block
Facegen ID 3AFC	Sequential	800	4000	Forced Choice	Keypress	72	Interleaved Blocks	7	33	Yes - Within Block
Harvard ID Same/ Different	Sequential	500	500	Same/Diff	Keypress	60	Interleaved Blocks	8	50	Yes - Within Block
Photo to Two-Tone ID	Simultaneous	5000	Not Applicable	Forced Choice	Keypress	110	Interleaved Trials	12	33	Set Order
Face Matching - Top Half	Sequential	1000	4000	Forced Choice	Keypress	120	Interleaved Blocks	15	33	Set Order
Face Matching - Bottom Half	Sequential	1000	4000	Forced Choice	Keypress	120	Interleaved Blocks	15	33	Set Order

All tasks except for one task were organized into blocks of either upright or inverted trials. On Photo to Two-Tone ID, upright and inverted trials were interleaved on a trial-by-trial basis. Trials were organized in blocks consisting of either ten trials with upright stimuli or ten trials with inverted stimuli. Prior to each block, participants were told if a block involved upright faces or inverted faces. The order of trials within a block was randomized for four tasks whereas a set order within blocks was used in three tasks. Task position refers to the position of the task among all the tasks.

Detection of Thatcherized faces

The Thatcher task was run twice, once with keypress responses and then with voice responses. In each trial, participants were presented with three test faces simultaneously. Two of the faces were unmanipulated. In the third face, the eyes, the mouth, or the eyes and mouth were rotated 180° relative to the rest of the face (Figure 4A). Participants were shown examples of upright and inverted examples of Thatcherized faces at the start of the task. Prior to the start of the task, they were instructed to indicate which one of the three test faces looked strange. Upright and inverted blocks were interleaved.

Details for Thatcher tasks

Thatcher Perception

Task	Presentation of Stimuli	Presentation Duration (ms)	Decision	Response	# of Trials	Up/Inv Presentation	Task position	Chance Accuracy (%)	Randomization
Thatcher Keypress	Simultaneous	4000	Forced Choice	Keypress	60	Interleaved Blocks	4	33	No
Thatcher Microphone	Simultaneous	4000	Forced Choice	Voice	60	Interleaved Blocks	16	33	No

Trials were organized in blocks consisting of either ten trials with upright stimuli or ten trials with inverted stimuli. Participants were able to respond even after the triplet of test faces had been removed from the display.

QUANTIFICATION AND STATISTICAL ANALYSIS

For each type of task and for each participant, we created a combined result across all tasks of the same category (face detection, face identity matching, and Thatcher detection). The combined percent correct values and combined response times values were calculated by taking the weighted average of the individual test data for each category of tasks. The weight for each test is the number of trials in the test. Below is a formal expression of the calculation used to generate the combined values:

$$x_c = \frac{\sum_{i=1}^{n} (T_i x_i)}{\sum_{i=1}^{n} T_i}$$

x_c denotes the combined score for one participant for a specific category of test. n is the total number of tests in that category, x_i is the score from test i, and T_i is the number of trials for test i.

We computed FIE for each test by comparing the performance on upright trials with that of inverted trials. Higher FIE can be interpreted as superior performance with upright faces. For accuracy, we defined the FIE as upright accuracy *minus* inverted accuracy. For reaction times, we defined the FIE as inverted reaction times *minus* upright reaction times. For controls, we tested whether the FIEs were significantly above zero using one-sample *t*-tests.

To compare Claudio's performance to the controls' performance on the same task, we used statistical tests designed to compare results from a single neuropsychological participant to a control group. These tests are less likely to produce type I errors than traditional methods when the control sample size is relatively small ($N < 50$).[33,64] In particular, we used Crawford and Howell's (1998) modified *t*-test to compare Claudio's FIE in each task (separately for accuracy and RTs) to the FIEs of the controls.[64,65] We also used the same test to compare Claudio's performance to control performance in different conditions (for example, Claudio's accuracy upright for face detection with the control groups' upright accuracy for face detection).

The Revised Standardized Difference Test (RSDT)[33] was used to compare cross-task performance differences between Claudio and the controls (e.g., the difference between Claudio's FIE on Thatcher tasks and detection tasks versus the difference between controls' FIE on Thatcher tasks and detection tasks). All two-tailed p values for these tests are reported in Table S1.

All statistical analyses were run in R 4.0.5[66] using scripts that implement the algorithms described in the papers that introduced these statistical tests.[33,64] All scripts are available online at figshare.

Data sharing plan

The datasets from the current study have been deposited in a public repository. Database: https://figshare.com/projects/The_Development_of_Upright_Face_Perception_Depends_on_Evolved_Orientation-Specific_Mechanisms_and_Experience/150507.