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Research report

Perceptual dominance of oriented faces mirrors the distribution of orientation tunings in inferotemporal neurons

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Abstract

In three experiments participants viewed pairs of overlapping transparent faces, with one face upright and the other oriented, and they reported which face was dominant. In each trial, an upright face was presented with a face at 45, 90, 135 or 180°, with transparency set using a linear weighted algorithm, so that relative contrast across faces was biased in favour of oriented faces. Exposure duration was restricted in experiment 1 to 250, 500 or 1000 ms, but was unlimited in experiments 2 and 3. Adults were tested in experiments 1 and 2 and children aged 6–9 years of age were tested in experiment 3. Irrespective of exposure duration, the results showed the probability of dominance being ceded by oriented faces to upright faces was a function of orientation. In comparable conditions, the function found with young children was flatter than with adults. These patterns, and those of earlier perceptual studies, can be explained by the distribution of different orientation tunings found in physiological studies of inferotemporal cortex in macaques.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Face perception; Overlapping faces; Inferotemporal neurons; Development

1. Introduction

Research has shown that upright (or close to upright) faces are processed in a holistic manner, whereas inverted faces (or those close to being inverted) are processed in a piecemeal manner [5,21]. Research exploring face processing has generally divided orientation into only upright and inverted categories and has not considered the impact of orienting faces within the intermediate range between upright and inverted orientations. The few studies that have investigated the impact of orientation on face processing (other than upright and inverted) have, however, produced consistent results. Jeffreys [9] recorded evoked potentials following passive viewing of faces and demonstrated that the peak latency of the vertex positive potential (VPP) found when viewing faces changed with orientation. The time taken to generate VPPs increased linearly for faces shown at orientations up to or slightly beyond 90° and decreased marginally beyond this point and up to 180°. In contrast, this study found no effect of orientation on the amplitude VPPs. Sturzel and Spillman [20] used the method of limits to determine the angle that ‘Thatcherised’ faces [23] lost their grotesque appearance. In this study, the shift in perception from grotesque to non-grotesque occurred at ~110°, although response time (RT) data from Lewis [13] using a similar task suggested a gradual loss in perception of the illusion from ~60 to 135°.

In an unpublished study that also aimed to assess the impact of orientation on face processing, Martini et al. [14,15] allowed participants to set the relative contrast of pairs of overlapping transparent faces until they appeared bi-stable. In their task, one face was always presented upright and the same face was presented at one of a number of orientations away from upright (see Fig. 1 for an example of a stimulus). The results of this study demonstrated that in order to achieve bi-stability the

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Fig. 1. Example of stimulus similar to that used by Martini et al. [14] and those used in experiment 1.

relative contrast of the oriented and upright faces had to increase in favour of the oriented face, with the relative increase tapering off at orientations ±90° from upright. These results were unchanged whether faces were lit from above or below. When scrambled faces were used instead of photographs of real faces, the result was very different: No change in relative contrast was necessary to compensate for increasing orientation. Confirmation that overlapping faces that are close to upright and of similar luminance exhibit bi-stability can be found in the work of Boutet and Chaudhuri [2]. Using exposures longer than 1 s, they demonstrated that faces that are 45° to the left and right of upright will exhibit bi-stability with each face perceived in turn. In contrast bi-stability was not found for faces close to being inverted or upright faces presented for 1 s or less.

These sets of research findings suggest a common mechanism may underlie (i) the impact of intermediate orientations between upright and inverted faces on the production of VPPs, (ii) the perception of the Thatcher illusion and (iii) the relative contrast required for equalising the salience of oriented and upright overlapping transparent faces. It is likely that these results reflect reduced numbers of neural cells sensitive to whole faces (i.e. those cells performing holistic processing) at orientations away from upright. In support of this proposition Tanaka et al. [22] performed single cell recordings for face sensitive cells in macaque inferotemporal (IT) cortex. Of the 21 cells whose preferred orientation was determined, 12 preferred upright faces, five preferred faces at 45°, two preferred faces at 90°, one preferred faces at 135° and two preferred faces at 180°. (It is important to note that 11 cells were tested in detail and demonstrated coarse coding and some had complex tuning curves.) If an equivalent area is involved in basic face processing in humans (the fusiform face area (FFA) [7]), then the distribution of preferred orientation of face cells will probably be similar.

Assuming a similar distribution of orientation-sensitive face cells in humans and macaque monkeys, this leads to explanations of the effect of increasing orientation on latency of peak amplitude on VPPs, the perceived magnitude of the Thatcher illusion and the increase in relative contrast required for oriented faces to compete with upright faces in transparent displays. The Thatcher illusion will not be perceived in oriented faces beyond some ranges because of the small numbers of cells processing holistic facial information. The rate of production of VPPs can be accounted for by making the further assumption that overall firing rates will be higher for larger than smaller populations of cells [17]. Similarly, for oriented faces to reach threshold before upright faces in transparent displays, relative contrast must be adjusted as stimulus intensity influences the firing rates of neurons [11]. It is, therefore, apparent that consideration of the relative number of cells sensitive to faces at varying orientations is sufficient to account for the range of behavioural data describing how face processing is affected by increasing orientation.

In summary, the correspondence between electrophysiological, behavioural and neurophysiological data suggests measurement of a common system. The available behavioural data allowing estimates of the effect of orientation on face perception to be made are, however, minimal [13,14,20]. The aim of the present study is, therefore, to explore further the impact of orientation on face perception by considering participant's perception of dominance in pairs of overlapping, transparent faces. In a competition between overlapping stimuli, the advantage is likely to go to the stimulus that can most easily be perceived as a complete unit, and thus this measure was expected to reflect the IT cells that encode faces holistically. Following previous findings it was anticipated that when participants were presented with pairs of overlapping and transparent faces, and asked to report on dominant faces, the competition between faces will be a function of their relative orientations. Specifically, oriented faces will cede dominance to upright faces according to a non-linear function with an initial steep decline in dominance up to 90° being followed by a more gradual loss of dominance beyond 90°.

2. Experiment 1

Experiment 1 asked participants to judge which of two faces was dominant in pairs of overlapping faces. The choice was biased in two ways. Firstly, one face in each pair was always upright and the other presented at 45, 90, 135 or 180°. Second, the relative contrast of the faces was manipulated so that oriented faces contributed 55% to the transparent face-pairs. Setting relative contrast in favour of oriented faces at this level allowed a measurement of the impact of increasing orientation on perceived dominance without the selection of the upright faces assuming a probability of 1.0. Previous research has demonstrated that bi-stability in transparent face images is rare at or below 1 s [2]. The present experiment was run at 250, 500 and 1000 ms in order to explore initial dominance states more fully.

2.1. Method

2.1.1. Participants

A total of 24 undergraduate students from the University of Southampton participated in this study. All had normal or corrected-to-normal vision and received course credits for taking part in the experiment.

2.1.2. Stimulus materials

A total of 20 male faces were obtained from the Stirling picture database. Using Corel Photopaint faces were extracted from their background and mounted on a uniform white background. Faces were rotated and re-sized so that eyes were level and the inter-pupillary distances were equalised and set to 50 pixels. The face images were all in 256 grey-level format and normalised so that they were 175 pixels wide×250 pixels high.

The 20 faces were then sorted into pairs approximately matched for luminance after measuring the luminance of each face. These face-pair images were manipulated using a weighted linear interpolation algorithm such that oriented faces contributed 55% of the available stimulus energy to the final face-pair images. These face-pairs were then used to create eight composite images per face-pair with one face anchored to upright while its partner was oriented to 45, 90, 135 and 180°. This led to a set of 80 overlapping face-pair images. All composite images were then pasted into an annulus with a radius of 70 pixels (Fig. 1). The visual angle of the inside of the annulus was 3°.

2.1.3. Apparatus

Stimuli were presented on a Pentium 4 Viglen Genie PC and monitor. Stimuli were presented and responses recorded using the SuperLab programming environment. Responses were made using the two outer keys of a 610 Cedrus response box. Participants sat with their head fixed in a chin rest positioned 100 cm from the screen. Initial luminance values were measured using a Minolta CS-100.

2.1.4. Procedure

Participants were told that for each trial they should look at the fixation cross and study the image of transparent face-pairs following fixation. Transparent faces were presented for either 250, 500 or 1000 ms, followed by a pattern mask composed of scrambled facial features. Participants were instructed to select either the upright or oriented face on the basis that they were the dominant face in each image. If they judged faces to be of equal dominance, then they were instructed to choose either upright or oriented responses at random. Trials began with the fixation cross 1 s after the response to the previous trial had been made. The order of completion of the exposure duration conditions was controlled using a Latin square.

2.2. Results

The results were expressed in terms of the selection of oriented faces. Given that these data are bounded, they were transformed according to the formula $DV = \log(X/(20 - X))$, where DV=dependent variable and X= condition score. As scores at ceiling would generate a division by zero error in this formula, we planned to replace any ceiling scores of 20 with a value of 19.9, however no participant generated a ceiling score in any condition of experiment 1. The transformed data were analysed in a 3 (Exposure Duration: 250 vs. 500 vs. 1000 ms)×4 (Orientation of non-upright face: 45 vs. 90 vs. 135 vs. 180°) ANOVA repeated over both factors).

The main effect of Orientation was significant, $F(3,69) = 19.78$, $P < 0.01$, but neither the main effect of Exposure Duration nor the interaction between Exposure Duration and Orientation were significant, $F(2,46) = 1.04$ and $F(6,138) = 1.64$, respectively (Fig. 2). Bonferroni-corrected t-tests demonstrated no significant difference between 45 and 90° ($t(23) = 2.32$) or 135 and 180° ($t(23) = 1.74$), but there was a sharp decline between 90 and 135° ($t(23) = 8.27$, $P < 0.01$). In addition, these same data were analysed in terms of polynomial contrasts as the hypothesis that perception of dominance in oriented faces reflects the orientation tuning of face sensitive cells in IT implies a non-linear trend across the data points measured. Analysing the effect of Orientation using polynomial contrasts

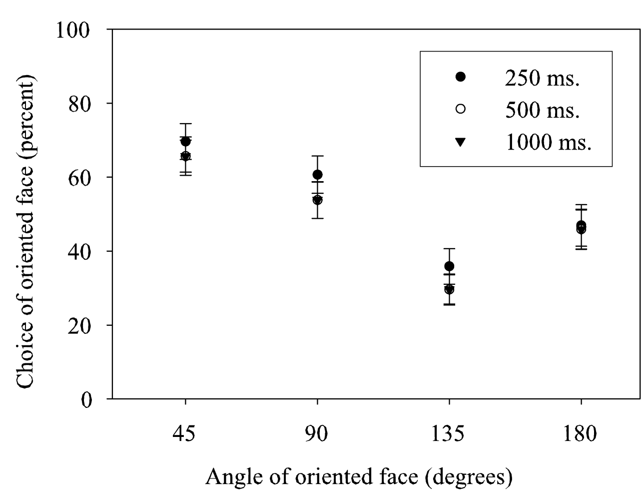

Fig. 2. The % of oriented faces chosen in the different conditions of experiment 1.

revealed significant linear, quadratic and cubic components ($F(1,23)=33.58$, $F(1,23)=5.33$ and $F(1,23)=32.18$, $P<0.01$, $P<0.05$ and $P<0.01$, respectively).

2.3. Discussion

The effect of orientation remained relatively constant between 45 and 90° but fell rapidly up to 135°. These data suggest that between 90 and 135° faces lose their ability to grab attention because their presence is being signalled weakly compared to the presence of upright faces. The orientation range through which this decline occurs is consistent with previous studies in the literature. It is suggested that there is a decline in the number of face sensitive cells tuned to faces presented at orientations between 90 and 135°. The effect of this decline in the number of face sensitive cells is to weaken holistic processing [20], to slow VPPs [9] and to influence dominance relationships in pairs of overlapping and transparent faces [14].

This pattern of data can be explained in other ways. For example, it is possible that these effects are not specific to faces. In this case, the resolution of dominance within any pair of overlapping images might generate the same function irrespective of the identity of the stimulus. A control experiment demonstrated, however, that this explanation of the results is unlikely. A group of 12 participants were presented with cartoon car stimuli constructed in an identical manner to those in experiment 1. These stimuli form a good control to the face stimuli since they are normally seen in one orientation (i.e. upright), moreover they had been given some facial-like features (Fig. 3). If it was the case that all stimulus sets or any mono-oriented stimuli (e.g. houses, cars, etc.) lead to effects of orientation like that found in experiment 1, then these stimuli should also generate similar effects of orientation. The results of the 12 participants are shown in Fig. 4. As in experiment 1, the main effect of Orientation was significant, $F(3,33)=56.22$, $P<0.01$, and there was no effect of Exposure Duration, $F(2,22)=1.1$, and no interaction between Orientation and Exposure Duration, $F(6,66)=1.6$. There was no significant effect of orientation up to 90° and only a modest one at 135°. Unlike the results of experiment 1, however, participants in this control condition almost always reported that the upright car was dominant in the 180° condition, and comparisons between this and all other conditions were significant.

Formal comparison of the face and car condition in a between-subjects ANOVA clarified the differences between face and car conditions with a significant interaction between orientation and stimulus type (Face vs. Car), $F(3,102)=35.1$, $P<0.01$. Pairwise comparisons at each orientation using Bonferroni-corrected *t*-tests, demonstrated no significant difference between choice of the oriented face or car in the 45° condition, but significant effects in all other conditions. The result in the 45° condition is important because it demonstrated that differences in the effects of orientation in the face and car condition do not occur because of fundamental differences in the discrimination of overlapping faces and cars. At least in one condition, the biasing of the images in favour of the oriented stimulus is equivalent in faces and cars. Therefore, the differential loss in bias with increasing orientation is likely to be related to the categorical identity of the stimuli. If it was related to some uncontrolled (and unknown) physical difference between cars and faces, this effect would only emerge beyond 45°.

Fig. 3. Example of the cartoon car control stimuli.

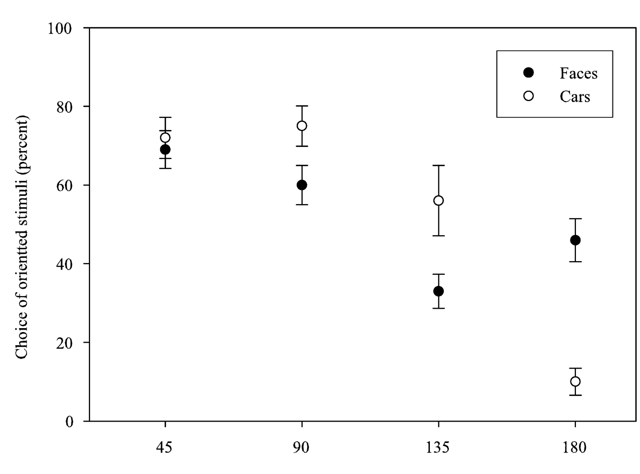

Fig. 4. The % of oriented cars chosen in the control experiment of experiment 1.

3. Experiment 2

The results of experiment 1 are consistent with the idea that increasing relative contrast might compensate for a loss in the dominance of oriented faces, as the difference between upright and oriented faces increases [14]. While the results are highly suggestive of this effect, it is not conclusively demonstrated. This is because relative contrast was not manipulated in experiment 1.

Experiment 2, therefore, investigated whether manipulating the transparency of composite images using 55, 60 and 65% transparency conditions would provide evidence that increasing relative contrast can compensate a loss of sensitivity to faces oriented beyond 90°. The relative effect of orientation on the probability of choosing oriented faces was the focus of comparison in different transparency conditions.

Two other changes to the methodology of experiment 1 were also made. First, stimuli were presented until response in order that participants could be encouraged to search for and find both faces in the overlapping images before deciding which face, over time, dominated. Second, to encourage this search-and-find process, full-luminance component images were also displayed on the screen simultaneously with targets in an arrangement that allowed a 2AFC decision to be made to either the left or right face.

The simultaneous presentation of composite and component images also allowed experiment 2 to address one further possible interpretation of the results of experiment 1. If the function relating choice to orientation is symmetrical around the vertical axis, then it would be an inverted W shape. These data have a similar form to RT data from mental imagery experiments on object recognition [10]. This alternative explanation raises the possibility that participants might have been rotating the oriented face to upright before comparing images. In this case, the effect of orientation could result from a reduction in image strength during transformation. Allowing participants to make a direct match between composites and components possible at all orientations (through simultaneous presentation of composite and component images) should remove this possibility.

3.1. Method

The apparatus was the same as in experiment 1.

3.1.1. Participants

A total of 30 undergraduate students from the University of Southampton were recruited as participants. All had normal or corrected-to-normal vision. Participants received course credits as an inducement to take part in the experiment.

3.1.2. Procedure

Participants were sat in a dimly lit room 100 cm from the computer screen. They were told that, for each trial, they should look at the fixation cross and study the transparent image of face-pairs following fixation. After determining whether the upright or oriented face was the dominant one in the image, they were asked to match this face to one presented in the pair of probe faces directly below (Fig. 5). On finding the match they responded with either the left or right response button. No restrictions were placed on re-sampling the target image after examining the probe faces or on the time taken choosing dominant faces. Participants were instructed that when faces were of equal dominance they should choose either the upright or oriented face at random. Trials began with the fixation cross 1 s after the response to the previous trial had been made. The order of completion of the transparency conditions was controlled using a Latin square.

3.2. Results

The results were expressed as in experiment 1 and analysed in a 3 (Transparency: 55 vs. 60 vs. 65%)×4 (Orientation: 45 vs. 90 vs. 135 vs. 180°) ANOVA repeated over both factors.

The main effects of Transparency and Orientation were significant, $F(2,58)=96.59$ and $F(3, 87)=43.95$, both $P<0.01$ (Fig. 6). The probability of selecting the oriented face increased with transparency and tended to reduce with orientation. Specifically, Bonferroni-corrected *t*-tests revealed oriented faces to be selected significantly more frequently than upright faces in the 45° condition than in the 90° condition ($t(29)=8.6$, $P<0.01$). There were also strong trends showing oriented faces to be selected more often than upright faces in the 90° than the 135° conditions. The interaction between Transparency and Orientation did not reach significance, $F(6,174)=1.61$.

The data in the 45° condition, however, are problematic as 2/30 participants in the 55% transparency condition, 8/30 in the 60% transparency condition and 12/30 in the 65% transparency condition always selected the oriented face (i.e. performed at ceiling). This did not occur in any other orientation for any of the transparency conditions. Therefore, to overcome the problem caused by interpreting interactions (significant or otherwise) partially caused by data being at ceiling, the data were re-analysed excluding data from the 45° condition. In this analysis, the main effect of Transparency was significant, $F(2,58)=93.72$, but the main effect of Orientation just missed significance, $F(2,58)=2.8$, $P<0.07$. However, the interaction between Transparency and Orientation was significant, $F(4,58)=2.59$, $P<0.05$. Bonferroni-corrected *t*-tests conducted to examine the effects of orientation at each level of transparency demonstrated that oriented faces were selected more often in the 90° than 135° conditions in the 55 and 60% transparency conditions but not in the 65% condition ($t(29)=3.93$, 3.00 and 0.4, $P<0.01$, $P<0.01$, $P=$NS for the 55, 60 and 65% transparency conditions, respectively).

Fig. 5. Example of the face stimuli shown in experiment 2.

No other comparisons of neighbouring points were significant. Using polynomial contrasts to analyse the same data leads to significant linear, $F(1,29)=5.00$, $P<0.05$, and quadratic trends, $F(1,29)=6.32$, $P<0.05$, in the 55% transparency condition, only a significant quadratic trend in the 60% transparency condition, $F(1,29)=5.82$, $P<0.05$, and no significant trends in the 65% condition.

3.3. Discussion

The results of experiment 2 demonstrated that orientation affected the probability of choosing oriented faces in every transparency condition. Ceiling performance in the 45° conditions makes the exact form of the interaction difficult to interpret across the complete data set. However, re-analysis of data excluding those from the 45° condition demonstrated that transparency and orientation interacted. Given the relationship between transparency and relative contrast, the results are consistent with those reported by Martini et al. [14]. They suggest that to preserve the probability of choosing oriented over upright faces as orientation of the oriented face increases, the relative contrast of the images needs to be altered. The simplest account is that a fixed cell population fires to faces at each orientation in every transparency condition but that smaller populations of cells benefit more from higher levels of relative contrast than do larger populations of cells.

An important aspect of experiment 2 was that it would allow for competition between upright and oriented faces to emerge. The design of the experiment did not, however, force participants into viewing displays for extended periods of time. Previous work suggests that competition between overlapping faces emerges with exposure in excess of 1 s [2]. It is, therefore, important to show that RTs are greater than 1 s. RTs to choices of all oriented and upright faces are shown in Fig. 7. These data have been averaged across transparency conditions as each transparency showed effectively the same pattern of data. They show that RTs for choosing all faces increased as the orientation of the oriented face increased. RTs for choosing oriented faces were in a range between 1600 and 2200 ms

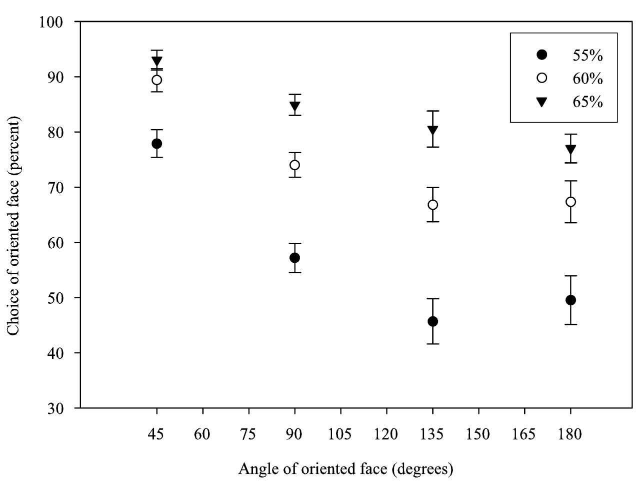

Fig. 6. The % of oriented faces chosen in the different conditions of experiment 2.

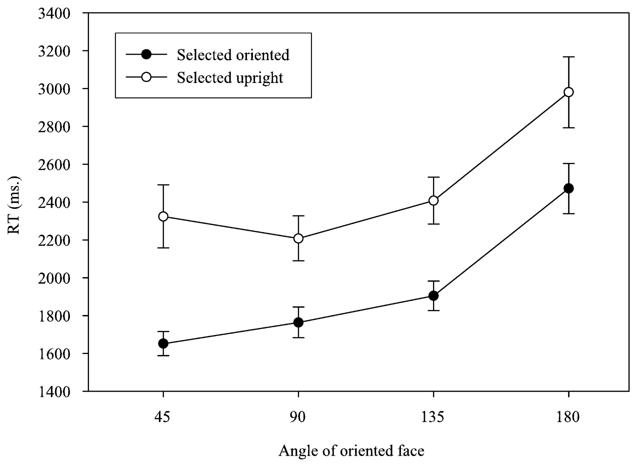

Fig. 7. RTs for choosing oriented and upright faces in experiment 2, averaged across different transparency conditions.

and RTs for choosing upright faces were between 2300 and 2900 ms. The data are interpreted as showing that relative contrast biased the initial allocation of attention to oriented faces, but that upright faces could compete over time if the oriented face did not hold attention. The cost of switching from oriented faces and engaging on the upright faces was ~700 ms.

The functions reported in experiments 1 and 2 appear to differ. However, statistical comparisons across the 55% transparency condition of experiment 2 and all exposure duration conditions of experiment 1 (i.e. the only comparable conditions) show that only one comparison, the 1000-ms condition of experiment 1 versus experiment 2, is significantly different. All comparisons did reveal that participants were more likely to choose oriented faces in experiment 2 than experiment 1. It is suggested that any differences in the effect of orientation on the probability of choosing oriented faces is constant across tasks and exposure duration, and is caused by broadly-tuned cells requiring time to resolve into a global solution.

4. Experiment 3

The results of experiments 1 and 2 are consistent with the hypothesis that perceived dominance in pairs of overlapping, transparent faces can be predicted from known properties of the underlying neural populations of cells in an area (the FFA) performing basic face processing. The probability of choosing oriented faces in pairs of transparent and overlapping faces declines up to ~135° but this reduction in probability can be overcome by increasing the relative contrast of upright and oriented faces. Further evidence that these results on perceptual dominance have any relation to the known properties of the response properties of face sensitive cells would be if a different set of findings occurred when a population was tested who were thought to differ in their basic face processing. In experiment 3, confirmatory evidence for this account is sought via a test of a specific prediction.

Previous research has shown that upright faces are not encoded holistically to the same extent in children under 10 years of age, compared with older children and adults. For example face recognition in young children is less affected by inversion [4,16]. In addition, young children process faces less holistically compared with older children and adults [3,6]. Presumably, these differences occur because long-term neurobiological re-organisation has yet to lead to the development of large populations of orientation-tuned face sensitive cells [1]. If orientation-tuned face-sensitive cells are not fully developed in young children, then dominance functions for this group should differ predictably from those of adults. Specifically, orientation should have a lesser impact on perceived dominance in young children, compared with adults and there should be no interaction with relative contrast. This result would be consistent with the proposition that dominance responses in this group are primarily driven by cells not specialised for face processing.

In experiment 3, a group of 30 children (aged 6 years to 9 years 5 months) performed the same conditions as in experiment 2 and their data were compared with that of the adults tested in experiment 2.

4.1. Method

All the details were as reported in experiment 2.

4.1.1. Participants

In addition to the 30 adults tested in experiment 2, 30 children between the ages of 6 and 10 were tested (mean age = 8 years 3 months, SD 17.17 months). Children were recruited via a local primary school and written informed parental consent was obtained.

4.2. Results

The data were analysed as in experiment 2 and first for the children alone in a 3 (Transparency: 55 vs. 60 vs. 65%) × 4 (Orientation: 45 vs. 90 vs. 135 vs. 180°) ANOVA repeated over the Orientation factor.

The main effects of Transparency and Orientation were significant, $F(2,58) = 62.72$, $P < 0.01$ and $F(3,87) = 52.34$, $P < 0.01$ (Fig. 8). The interaction between Transparency and Orientation was significant, $F(6,174) = 7.69$, $P < 0.01$. The probability of choosing oriented faces increased with transparency. Participants were more likely to select oriented faces in the 45° condition than in other orientations and this was true in all conditions. Analysing the interaction between Orientation and Transparency using Bonferroni-corrected *t*-tests demonstrated that there were no further effects of orientation in the 60 and 65% transparency conditions. In contrast, in the 55% condition, choices favoured the oriented face significantly more at

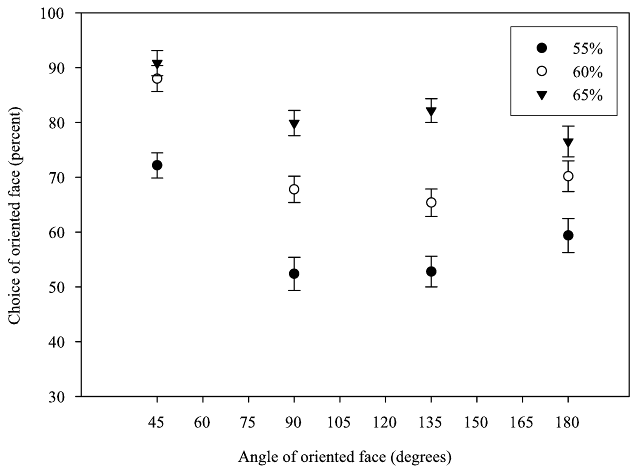

Fig. 8. The % of oriented faces chosen in the different conditions of experiment 3.

180 than at 135° ($t(29)=3.07$). There was no significant difference between choices at 90 and 135° ($t(29)=0.08$).

As in experiment 2, data in the 45° condition are compromised by a number of participants scoring at ceiling (0/30, 7/30 and 13/30 in the 55, 60 and 65% transparency conditions, respectively) although scores at the other orientations are not compromised. Dropping this condition from the analysis and re-analysing the data led to a significant effect of Transparency, $F(2,58)=56.4$, $P<0.01$, but no main effect of Orientation, $F(2,58)<1$. The interaction between Transparency and Orientation was also significant, $F(4,116)=4.59$, $P<0.01$. The Bonferroni-corrected *t*-tests demonstrated no significant effects of Orientation in the 60 and 65% transparency conditions. In contrast, in the 55% condition, although oriented faces were not selected significantly more often than upright faces when comparing 90° and 135° conditions ($t(29)=0.08$), they were selected more often at 180 than at 135° ($t(29)=3.07$, $P<0.01$). Analysing the same interaction using polynomial contrasts demonstrated significant linear and quadratic trends in the 55% transparency condition ($F(1,29)=4.4$ and $F(1,29)=4.2$, both $P<0.05$, respectively) but no significant effects of orientation in either the 60 and 65% conditions.

Comparisons of the effects of Orientation between the child and adult samples were made in two ways. First, comparison was made across all transparency conditions but omitting the 45° condition because of ceiling levels of performance (only those effects of Orientation interacting with the Age Group factor are reported). In this analysis, Age Group (Child vs. Adult) interacted with Orientation, $F(2,116)=3.66$, $P<0.05$. As can be seen from the breakdown of results in experiments 2 and 3, increasing orientation led to a lower probability of selecting oriented than upright faces in adults, especially between the 90° and 135° conditions. In contrast children were more likely to select oriented faces than upright faces in the 180° than the 135° conditions.

The second analysis comparing adults and children was across all orientations but limited to the 55% transparency condition as this condition contained only two participants (both adults) performing at ceiling. The results of this analysis demonstrated a significant interaction between group and orientation, $F(3,174)=6.99$, $P<0.01$. Bonferroni-corrected *t*-tests examining effects of orientation at each level of transparency demonstrated significant differences in the likelihood of selecting oriented faces in the 45° and 90° conditions for both adults and children ($t(29)=5.65$ and $t(29)=3.05$, both $P<0.01$, respectively). The difference between the 90° and 135° conditions was significant for adults only ($t(29)=3.93$ and $t(29)=-0.83$, $P<0.01$ and NS, respectively). The difference between selection of oriented faces in the 135° and 180° conditions was only significant for children and not adults ($t(29)=3.07$ and $t(29)=0.08$, $P<0.01$ and NS, respectively). Analysing this same interaction using polynomial contrasts led to significant linear and quadratic components for both adults and children ($F(1,29)=34.64$, $F(1,29)=20.10$, $F(1,29)=15.38$, $F(1,29)=51.52$ for adults and children, linear and quadratic components, respectively). In addition, children also generated a marginally significant cubic component than did not approach significance in adults ($F(1,29)=4.07$ and $F(1,29)=<1$, $P=0.05$ and NS, respectively).

4.3. Discussion

The results of experiment 3 suggest an interpretation consistent with the hypothesis that cells responsive to oriented whole faces are distributed differently in young children than in adults. First, the effect of orientation in the 55% transparency condition is such that the probability of selecting oriented faces declines between 45 and 135° but not between 135 and 180° with adults. In contrast, with young children, although the probability of selecting oriented faces reduces between 45 and 90°, there is no change between 90 and 135°. Furthermore, young children are more likely to select oriented than upright faces at 180 than 135°. Together, these data suggest that adults have more broadly-tuned cells around upright faces but with little sensitivity to inverted faces. In contrast, young children have a relatively narrow tuning for upright faces but also have a capacity to detect inverted faces. Second, the failure to find an effect of orientation beyond 45° in the 60 and 65% transparency conditions in children contrasts with adult performance in which only the 65% condition showed no effect of orientation beyond 45°. Therefore, the results of the experiment on young children are consistent with the dominance task being sensitive to the distribution of orientation-tuned face cells across child and adult groups.

5. General discussion

The results of the present experiments demonstrated that when transparent faces overlap, the probability that oriented faces dominate over upright faces varies as a function of the orientation of the oriented face. Experiment 1 showed that when the exposure duration of stimuli was limited to below 1 s, there was a steep decline in the probability of choosing oriented over upright faces between 90 and 135°. This effect was specific to faces and was not found with cartoon cars. Experiment 2 showed similar results when participants viewed images until they themselves were satisfied that dominance had been achieved.

The findings of experiments 1 and 2 are interpreted as showing the relative numbers of face sensitive cells, probably in the FFA, for detecting the presence of faces and coding them holistically that are tuned to respond to faces at particular orientations. This explanation is consistent with that given to related experiments [13,20]. It is also consistent with another result from experiment 2 showing that transparency condition interacted with orientation. This result can be predicted because increasing relative contrast and population densities should trade-off against each other assuming a response threshold.

The effects of orientation and relative contrast argue strongly that choice in the overlapping faces task is influenced by the relative densities and activation levels of populations of face sensitive cells. These data are, by themselves, novel and provide important data on how face detection is influenced by orientation and contrast. However, perhaps more important is the demonstration that behavioural data such as these can be used to reflect neurophysiological organisation, and can detect differences in this organisation across populations. Experiment 3 pursues this idea using child participants and the results suggest a different distribution of orientation-tuned face cells in children than adults. Further studies must explore the transition from the tuning curves found with young children to those found with adults. The suggestion here is that it should be possible to measure the impact of long-term experience on the neurophysiological organisation of the face detection system using the overlapping faces task.

The results from some earlier studies, such as the peak latencies of VPPs in response to faces presented at different orientations and the loss of the Thatcher illusion with increasing orientation, can be accounted for simply by considering the total activation triggered across all the broadly-tuned face cells by the stimuli in each condition. Accounting for the results from the current experiments (and those from Refs. [2,14]) is more complicated, however, because in these studies two faces appear simultaneously. If two overlapping face stimuli were presented to a collection of independent coarsely-coded orientation tuned cells, the resulting activation pattern would represent a single face at some orientation intermediate between presented faces (Fig. 9). In other words it would generate a form of illusory conjunction of the two orientations. Does this fact cause a problem for explaining the results of the present experiments by referring to activation of orientation-tuned face cells? In fact, there is evidence that the FFA responds in a winner-takes-all manner [24]. In their study Tong et al. demonstrated that VPP activity corresponds to attended faces, and was not affected by unattended faces presented on the retina when faces were shown under conditions of binocular rivalry. The competition between the overlapping faces in the current experiments could be similar to the competition between stimuli from different eyes in the study by Tong et al., with winners changing over time through bottom-up satiation of neurons or top-down exploration of alternate figure-ground assignments [12]. Thus there are two properties that a neural network must have in order to account for the different face perception studies mentioned here. First, the strength with which a face at a particular orientation can be represented depends on the number of cells in the network tuned to respond to that orientation. Second, the network must be constructed so that when multiple faces appear, only one face at a time will be activated.

One might speculate on a number of different mechanisms through which this winner-takes-all competition might be implemented within the FFA. Although a solution based on the satiation of neurons is possible, it is more likely that attention is involved. For example, attention

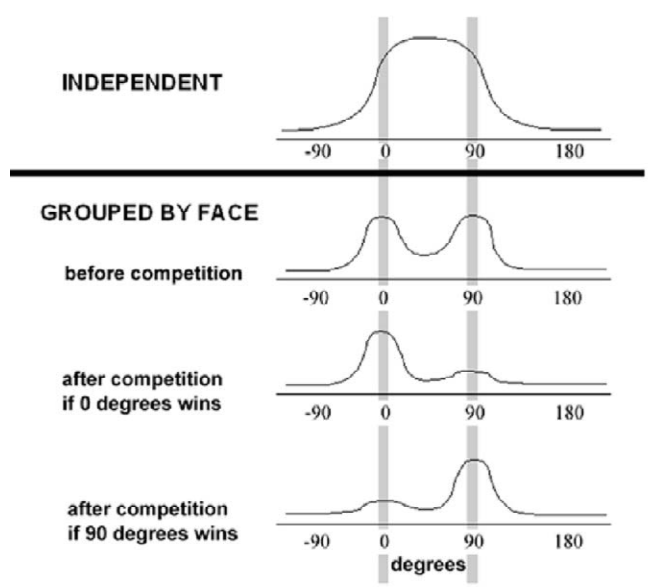

Fig. 9. The top graph shows the summed response across an entire collection of broadly-tuned face neurons when the response of each neuron is independent of the others. The stimulus is composed of two faces at 0 and 90° presented simultaneously. The two orientations are marked by grey bars. The lower three graphs show the responses if all the neurons responding to a single face are linked together and allowed to compete against another set of neurons responding to the other face. The final configuration depends on the outcome of the competition.

could be used to select locations (or objects) from the perceptual data created by overlapping objects. Selection might require dual activation between top-down object representations and features in the stimulus. Illusory faces at intermediate orientations might be activated at first, but will not be sustained by feature information and will eventually be inhibited. A model using this type of location-independent selection via object representations to guide location selection in letter perception has been presented by Shi and Cave [18]. In this account, orientation sensitive face cells in the FFA would act as high level face-templates facilitating feature encoding.

A second possible account is that inhibition of orientations close to the most highly activated orientations might be used to stop intermediate orientations ever gaining activation. Evidence has been reported in primates for this type of ‘flanking’ inhibition playing a role in modifying the tuning curve of cells in V4, while performing a difficult or easy orientation discrimination task [19]. It is also possible that neural synchrony might be used to maintain separate representations of the two different faces simultaneously. This dynamic binding would prevent the two representations from combining to form a representation at an intermediate orientation. Even though both orientations are represented, set phase relationships might allow only a single face to be attended to [8]. At present, there are no data to discriminate between these accounts, but modelling interactions between orientation sensitive face cells is a significant issue, given the data reported above.

The results of experiment 1–3 are consistent with the idea that a perceptual task involving competition between two faces can be used to measure the relative sizes of populations of orientation-tuned face sensitive cells. The results demonstrate that perceived dominance in pairs of overlapping, transparent faces is affected by orientation, and that this effect can be balanced by manipulation of relative contrast. The data are, however, limited by the number of orientations sampled. Despite the fact that only four orientations were used in these displays, the general form of the response function across different orientations contrast holds across different relative contrasts. This consistency suggests that a basic property is being tapped. We hypothesise that the property being measured is related to the relative density of orientation-tuned face cells sensitive to holistic properties of faces. If this is correct, it establishes an important correspondence between behavioural and physiological studies of face perception.

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