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Orientation tuning of human face processing estimated by contrast matching in transparency displays

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Abstract

Upright images of faces appear more salient than faces of other orientations. We exploited this effect in a titration experiment where faces were superimposed in transparency. By manipulating the physical contrast of the component images, we measured the degree of perceptual dominance as function of the orientation of the face in the image plane. From these measurements, we obtain the orientation tuning of face processing, which is well approximated by a Gaussian function with a SD of about 45 deg and mean centered on upright. Faces predominantly lit from above and from below produced very similar results. However, when presented with scrambled faces observers showed no orientation preference. We argue that these results can be explained by the existence of specialized face processing mechanisms with an orientation tuning with a bandwidth of approximately 90 deg, predominantly centered on the upright orientation and easily disrupted by alterations of the normal facial configuration.

Keywords: Human face processing; Configural processing; Holistic processing; Contrast matching; Orientation tuning

1. Introduction

Casual observations are sufficient to convince anyone that faces are harder to recognize when seen upside-down. Although this inversion effect for faces has been exploited as a perceptual illusion in the visual arts since classical times (Wade, Kovacs, & Vidnyansky, 2003), Yin (1969) was the first to document that the deficit observed for faces is disproportionately large when compared to the recognition deficit of familiar objects seen under comparable conditions. Evidence accumulated in the years following Yin's observations, with observers who are not experts with the target objects, supports the idea that the face inversion effect reveals the processing of a neural system and computational style specialized for face recognition and distinct from a more general object recognition mechanism (Kanwisher, McDermott, & Chun, 1997; Moscovitch, Winocur, & Behrmann, 1997; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). Whether experts do, or do not, process objects in the same manner as faces continues to be the subject of an intense debate (Gauthier & Tarr, 2002; McKone & Kanwisher, 2005). In the present study, we concentrate on the face inversion effect with the aim of quantifying the exact dependence on orientation of human face perception.

The relevant literature can be divided into two broad categories: studies that have found a linear decrease of performance with disorientation from upright (Collishaw & Hole, 2002; Lewis, 2001; Valentine & Bruce, 1988) and studies where the rotation effect was documented to be very nonlinear (McKone, 2004; McKone, Martini, & Nakayama, 2001; Murray, Yong, & Rhodes, 2000; Stuerzel & Spillmann, 2000). By linear decrease of performance we mean a gradual and progressive decline through 180 deg of rotation in the image plane, whereas by nonlinear decrease we mean a pattern of decline that reaches a

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plateau at orientations smaller than 180 deg, or an abrupt transition between qualitatively different percepts across a certain orientation.

Where linear effects were obtained, a frequent explanation has been the theory of mental rotation, whereby rotated faces need to be mentally normalized to the upright position before matching to stored memory representations (Rock, 1973), a variant of the align-then-match strategy of machine pattern recognition (Ullman, 1989). Assuming a constant speed of mental rotation this hypothesis could account for linear effects on reaction time measures, since it has been argued that the larger the rotation the longer the time to alignment and thus the time to respond. When accuracy is the dependent measure the mental rotation explanation is less clear. Conceivably, higher degrees of mental rotation could induce proportionately larger distortions of the face representation, which might perhaps hinder the accuracy of recognition in a linear manner.

In the case of nonlinear trends, a popular explanation invokes qualitatively different modes of processing for faces oriented upright and inverted. It is widely held that recognition of upright faces selectively taps into a highly sensitive mechanism that uses visual information in a ‘‘holistic’’ or ‘‘configural’’ manner, rather than solving the recognition task by utilizing independent processing subroutines for individual parts (McKone et al., 2001; Tanaka & Farah, 1993; Young et al., 1987). This second, ‘‘componential’’ mode of processing would reflect the default object recognition engine, which would be put at work for recognizing upside-down faces (Moscovitch et al., 1997). According to this account the disproportionately large face inversion deficit would result from the inability of the ‘‘holistic’’ face recognizer to process severely disoriented faces and from the poor ability of the general-purpose analyzer at recognizing exemplars of object categories, such as faces, which share a uniform subordinate structure.

In the present investigation, we consider the dependence of face discrimination on orientation in the image plane and ask the question of whether human face processing can be considered tuned for face orientation. By orientation tuning we mean a pattern of response consistent with the presence of an underlying mechanism selectively sensitive only to a limited range of orientations. The task that we use to measure orientation selectivity exploits a visual illusion whereby superimposing in transparency two images of the same face with different orientations may give rise to a rivalrous percept, where the two images alternate in their predominant salience. We show that the perceived salience of the two components can be equated by manipulating their physical contrast (Donnelly, Hadwin, Cave, & Stevenage, 2003; Martini, McKone, & Nakayama, 2001). From the measured contrast ratios for different orientation pairs we obtain an index of orientation sensitivity, which allows us to reconstruct the tuning curve of face perception.

2. General methods

2.1. Subjects

A total of 10 subjects were tested, all volunteers. Of these, seven were naïve as to the aims of the experiments, while the remaining three were the authors.

2.2. Stimuli

An example of the stimuli used in all experiments is shown in Fig. 1. Faces were digitally manipulated to replace the background or to eliminate the face contour and hairline.

Two images of the same face, identical except for an orientation difference, were overlaid digitally and displayed on the face of a computer monitor. The intensity of each pixel in the display was calculated by adding the intensities of corresponding pixels from the original images according to the following formula:

$$I_{1+2} = kI_1 + (1-k)I_2, \quad (1)$$

where k is a weighting parameter and I indicates the intensity of a given pixel. By manipulating parameter k the resulting image could contain only the first component ($k = 1$), only the second component ($k = 0$) or a mixture of both ($0 < k < 1$). This mixing rule is identical to the fading operation in morphing algorithms. The mean luminance and the RMS contrast (i.e., the standard deviation of the pixel intensities) of the final, composite image do not change with changes in k, whereas the mean luminance and contrast of each component image are linear functions of k. For example, when $k = 0.4$ the RMS contrast of image 1 is reduced to 40% and the contrast of image 2 is 60%, but the contrast of the composite image remains unchanged.

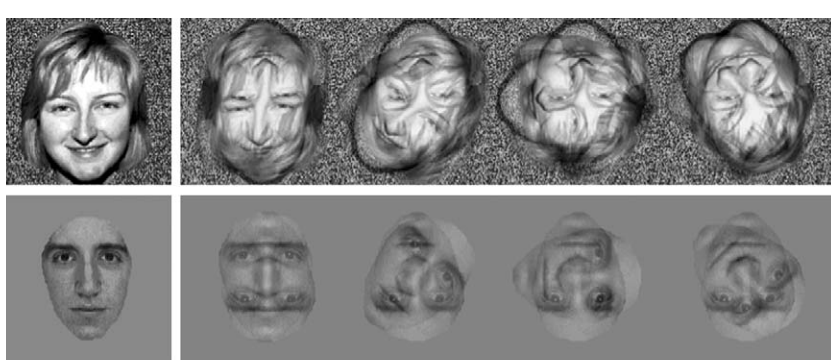

Fig. 1. Examples of stimuli used in experiments 1 and 2. Two identical images are superimposed in transparency at different orientations. Notice how the predominantly vertical image dominates the percept, appearing more salient and/or being seen for longer in foreground if perceptual rivalry is experienced. Throughout the text 0 deg orientation refers to the upright image and 180 deg orientation refers to the upside-down image.

2.3. Procedure

During preliminary observations subjects reported that certain orientation pairs, at certain contrast ratios, gave rise to spontaneous temporal alternations, similar to the rivalrous interpretations of ambiguous figures or the alternations experienced during monocular rivalry with spatial frequency gratings with small orientation differences. A description of such percepts with overlaid faces can be found in (Boutet & Chaudhuri, 2001). Subjects also reported that, when contrasts were equal, the face closer to upright would dominate the more disoriented face by appearing as having a higher salience or subjective contrast. To determine the point of subjective equality, subjects were instructed to try to balance the duration of such temporal alternations and/or equate the perceived salience by modifying the contrast ratio of the two images (changing parameter k in Eq. (1)). To do so they used computer key presses to trigger the online digital recombination of the component images according to a new contrast ratio. The display containing the mixed orientation pair was available for scrutiny and modification until the subject was comfortable with the contrast settings s/he chose. This final contrast ratio was then recorded and a new orientation pair of images would be displayed at a starting k of 0.5 ± 0.1 chosen randomly.

The order of presentation of the orientation pairs was randomized across blocks of measurements. For each orientation pair a minimum of 2 contrast ratio settings per subject were collected and averaged. Experiments were conducted at Harvard University and the Australian National University.

3. Results

3.1. Experiment 1: Equating salience across orientations

Salience matches were obtained for pairs of face orientations (from 0 to 180 deg in 45 deg steps clockwise) in a factorial design where each orientation was compared to all others. Tables 1 and 2 report data for the entire orientation matrix obtained from six subjects with the female face, which preserves the facial contour as well as hair, and from four subjects that were tested with the male face, which had been manipulated to remove the facial contour and hair (see Fig. 1). The reported figures are the average k values chosen by subjects, with values of 0.5 indicating equal percepts and values less or more than 0.5 indicating that image 1 elicited a stronger percept than image 2 or vice versa, respectively. There is a clear trend for k increasing toward 0.5 along the diagonals in the downward-right direction, indicating that perceptual dominance decreases with distance from upright, despite the fact that at each comparison the orientation difference was constant. There is also a clear trend for k decreasing across columns, an effect modulated in strength by rows (it is most evident for the first row), indicating that orientations closer to upright are perceived as more salient, but such effect diminishes non-linearly with distance from the canonical upright.

These results can be described more intuitively by plotting on a graph slices of data from Tables 1 and 2. Data in Fig. 2, left, are comparisons between the 180 deg orientation face and all others, thus representing a graphical description of the rightmost column of Tables 1 and 2. In Fig. 2, right, the comparisons are between the 90 deg face and all other orientations. The data is expressed as the k value (proportion of component 1 in the mix at the salience match) associated with the face orientation indicated on the abscissa. For both conditions, the results for the female (filled symbols) and male (hollow symbols) images do not differ significantly, although the male face tends to give more extreme results. The continuous line represents the best fitting second order polynomial (quadratic fit), which in both cases is statistically better than a first order nested model (linear fit) (on the left: $F(1,47) = 18.51$, $p < .0001$; on the right: $F(1,47) = 9.58$, $p < .003$), thus indicating non-linearity.

The results of this experiment demonstrate that whatever difference subjects perceive in the relative strength of the closer-to-upright image as compared to the further-from-upright one, this difference falls off nonlinearly with rotation. Further, compared to an inverted face, the salience difference has largely disappeared by the time the other face is rotated 90 deg from upright. The effect for the upright/inverted pair is substantial, amounting to an average physical RMS contrast ratio between the upright (0 deg) and inverted (180 deg) images of 0.67, an attenuation factor of about 1.5 (3.5 dB). Subjective reports suggest

Table 1
Results of experiment 1

Female face	Image 2				
	0	45	90	135	180
Image 1					
0		.467 ± .016	.443 ± .018	.445 ± .01	.432 ± .028
45			.49 ± .025	.468 ± .022	.472 ± .03
90				.507 ± .02	.505 ± .026
135					.52 ± .02
180					

The proportion of image 1 in the mixture at the saliency match is reported for image pairs across the entire orientation domain, for the female face. Figures represent mean results and 95% CI around the mean of six subjects. A proportion of .5 corresponds to a physical match, lower and higher proportions indicate predominance of images 1 and 2, respectively. Notice the tendency for the proportion to increase toward .5 along the diagonals in the downward right direction, indicating that the effect diminishes with greater rotations from upright, despite equal orientation differences.

Table 2
Results of experiment 1

Male face	Image 2				
	0	45	90	135	180
Image 1					
0		.43 ± .025	.417 ± .027	.417 ± .032	.377 ± .059
45			.425 ± .017	.43 ± .046	.45 ± .018
90				.475 ± .013	.49 ± .021
135					.512 ± .009
180					

The proportion of image 1 in the mixture at the saliency match is reported for image pairs across the entire orientation domain, for the male face. Figures represent mean results and 95% CI around the mean of four subjects. A proportion of .5 corresponds to a physical match, lower and higher proportions indicate predominance of images 1 and 2, respectively. Notice the tendency for the proportion to increase toward .5 along the diagonals in the downward right direction, indicating that the effect diminishes with greater rotations from upright, despite equal orientation differences.

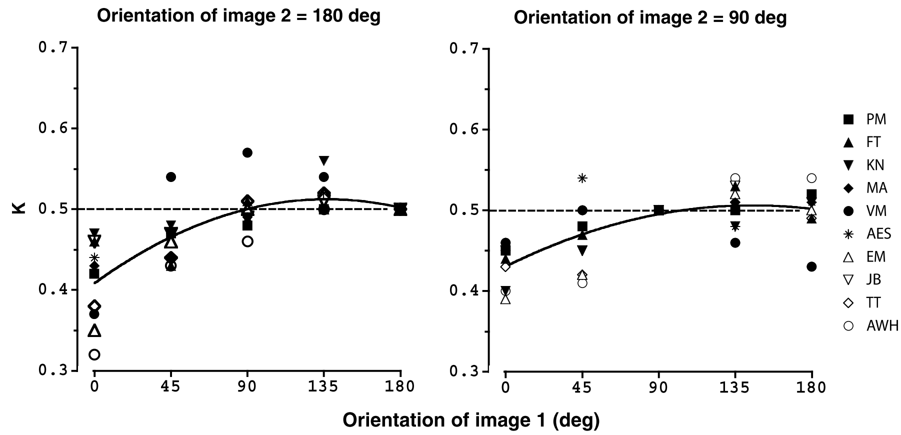

Fig. 2. Results of experiment 1. The proportion of image 1 in the mixture at the salience match is reported for image pairs where image 2 was presented at a fixed orientation. On the left, image 2 was inverted, whereas on the right it was presented rotated 90 deg. The solid line is the best fitting second order polynomial through the data. Notice the nonlinear dependency of the rotation effect. Solid symbols are individual subjects data for the female face, hollow symbols for the male face. The horizontal dashed line indicates equal physical contrast.

that such difference in contrast does not reflect a judgment made by comparing the local intensities of image patches, as subjects were aware that local features (for example, the eyes) in the images were significantly different in physical contrast. Rather, the differences likely reflect an effort on the part of the observer to achieve a balance between the relative strengths of the two facial images based on an internal metric of global perceptual salience. This observation led us to ask whether such effect would be abolished by disrupting the normal facial configuration, a hypothesis tested in experiment 2.

3.2. Experiment 2: Role of the facial configuration

In this experiment, we asked whether the facial configuration plays a role in inducing differences in salience across orientation and whether the effect observed in experiment 1 can be supported by individual features.

The procedure used in this experiment was in all respects identical to the previous one, but the stimulus was different. The male face image was manipulated by repositioning the features within the facial contour, as shown in Fig. 3.

Three observers (a naive subject and two of the authors) compared each orientation (from 0 to 180 deg in 45 deg steps) to all others in a factorial design. No single comparison yielded a k value deviating significantly from 0.5. Comparisons between the inverted face and all other orientations are shown in Fig. 3, right. It is apparent that the data do not deviate significantly from the equal contrast condition (dashed line) at all orientations.

Thus the salience effect depends on the configuration of the features and is not supported by the features in isolation. Consistent with this, subjective reports indicated that observers found it hard to visualize the scrambled image as a coherent whole and were compelled to make the contrast matches by trying to equate the physical contrast of individual features. Further, perceptual alternations between the two images were very weak or absent.

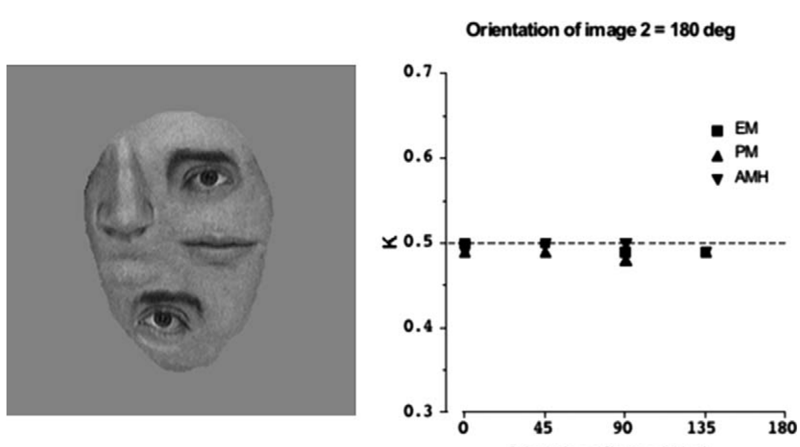

Fig. 3. Stimulus and results of experiment 2. The proportion of image 1 in the mixture at the salience match is reported for image pairs where image 2 was presented inverted. No deviation from the equal contrast condition (dashed line) is observed for any orientation pair.

3.3. Experiment 3: Effect of lighting direction

The 3D structure of visual objects must be inferred from their 2D projections on the retinae and from inherently ambiguous pictorial cues. One of the most common and powerful heuristics used by the visual system in forming a perceptual interpretation of an object is to assume that light comes from above. Given such an assumption, the relative pattern of shading can indicate, for example, whether different parts of a surface are concave or convex. As such, lighting direction plays a significant role in shaping the representation and recognition of 3D form.

When a face lit from below is inverted the pattern of lighting becomes consistent with the lighting from above rule. There is evidence that the inversion effect is reduced or eliminated in such cases (Johnston, Hill, & Carman, 1992). This effect has been explained by postulating an advantage in correctly deriving the 3D surface properties of the inverted, lit from below face. This advantage would compensate for the inability of properly apprehending the configural properties of the inverted face, thereby negating the effect of inversion. On the other hand, the recognition of an inverted, lit from above face is doubly impaired by the structural as well as lighting inversion.

Mindful of such lighting influences and noting that our stimuli were predominantly lit from above we wondered whether lighting direction might have contributed to the effect we were measuring. We therefore reran experiment 1 with the male face predominantly lit from below (Fig. 4, middle). Note that both images were photographed with some lighting also coming from directly in front of the face, in addition to lighting coming from above or below.

The results reported in Fig. 4, right, for a naïve subject and two of the authors demonstrate that lighting direction makes no substantial difference to the pattern of results for the two conditions, which are both consistent with a non-linear dependence of perceived salience on orientation. As such, lighting direction does not seem to be a major determinant of the perceptual salience asymmetries found in experiment 1.

3.4. Experiment 4: Derivation of orientation tuning curves

Experiment 1 showed that the effect on perception of the rotation of a face in the image plane is not a linear function of the degree of disorientation from upright. Only upright faces and to a diminishing degree also faces rotated up to, but not more than the horizontal orientation, are perceived as more salient. Thus the task at hand provides an opportunity to recover the tuning characteristic of face perception. This can be done by exhaustively comparing the inverted face with each other orientation and taking the reciprocal of the k value at the salience match as an index of sensitivity to that orientation.

To demonstrate this, we used the male face and a procedure identical to that employed in experiment 1, but with rotation steps of 10 deg.

Fig. 5, left, shows the face-tuning curve obtained from the two first authors acting as subjects. The solid symbols reported on the graph are the reciprocal of the k value for each image compared to the inverted face and the solid line is the best fit obtained by non-linear regression to the data of a Gaussian function of the form:

$$\frac{1}{k} = 2 + be^{-\frac{x^2}{2\sigma^2}}. \quad (2)$$

The choice of a Gaussian as a model for the tuning function allows for an easy estimate of the bandwidth. Thus, taking the quantity $1/k$ as an index of orientation sensitivity, the estimated orientation bandwidth of face perception expressed as 2σ in Eq. (2) is 90 deg (or 106 deg expressed as width at half height), centered on upright. This is roughly

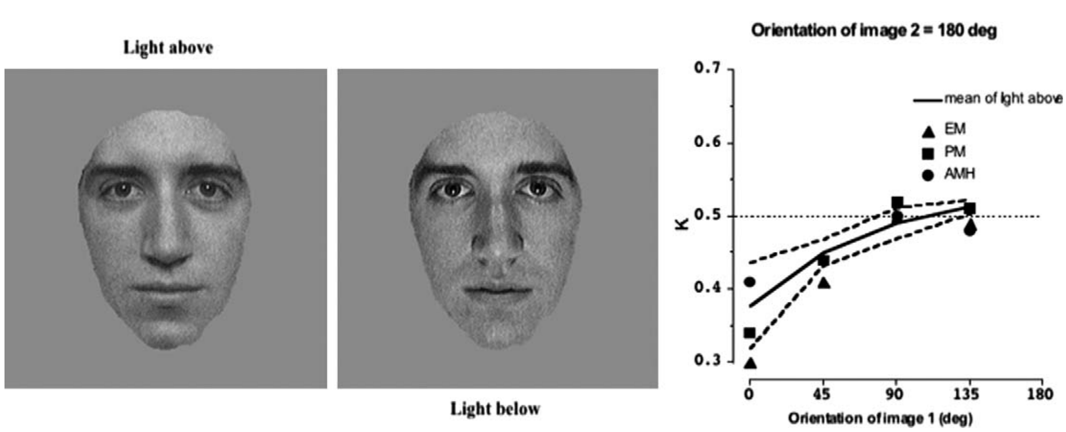

Fig. 4. Stimulus and results of experiment 3. The face on the left, used in experiment 1, is predominantly lit from above. The face in the middle, used in experiment 3, is predominantly lit from below. The graph on the right compares the results obtained with each face. Solid symbols indicate the proportion of image 1 in the mixture at the salience match for image pairs where image 2 was presented inverted in experiment 3 with the face lit from below. The solid line is the average data for the male face lit from above from experiment 1 and the dotted lines indicate the CI around the mean of those data. Results under different lighting conditions are comparable.

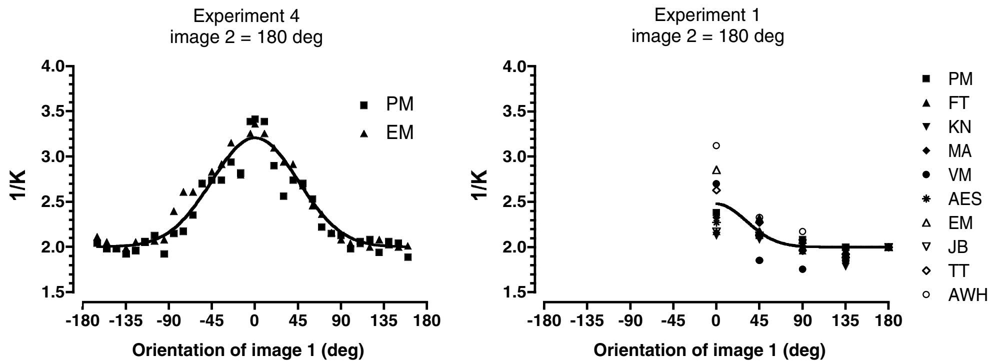

Fig. 5. Tuning curve of face perception. Data presented on the left are the results of experiment 4. For comparison purposes the results of experiment 1 are re-plotted in $1/k$ format on the right. Symbols correspond to the proportion of image 1 in the mixture at the salience match for image pairs, where image 2 was presented inverted. The continuous curve is a best fitting gaussian (Eq. (2)), with SD = 45.13 (CI 41.79–48.47), $R^2 = 0.92$ for experiment 4 and SD = 31.25 (CI. 21.16–41.33), $R^2 = 0.57$ for experiment 1.

equivalent to the bandwidth estimate obtained from re-plotting the results of experiment 1 as $1/k$, as shown in Fig. 5, right. The tuning estimated from the multiple subjects of experiment 1 is somewhat narrower and much worse in terms of goodness of fit, perhaps due to limited sampling; in addition, the gain is smaller on average, but similar to that of experiment 4 if only the data obtained with the same stimulus (the male face) are considered.

4. General discussion

4.1. Nonlinearity of the rotation effect

When asked to match the salience of two images of the same face superimposed in transparency at different orientations, subjects behave as if they perceived faces rotated up to 90 deg as more salient than faces rotated further. This is a nonlinear effect, which fades as the rotation of the face in the image plane approaches the horizontal and is absent for further rotations. As such, it should be grouped with recent behavioral results obtained in paradigms where subjects were asked to rate grotesqueness, to categorize the identity of morphed faces embedded in visual noise or to rate the appearance of a Mooney face (McKone, 2004; McKone et al., 2001; Murray et al., 2000; Stuerzel & Spillmann, 2000). Similar findings have also been reported anecdotally in the neuropsychological literature: for example, patient CK, who presents severe object agnosia, is able to recognize faces as well as control subjects provided the images are rotated less than 90 deg from upright (Moscovitch et al., 1997). In contrast, a number of reaction time studies (Collishaw & Hole, 2002; Lewis, 2001; Valentine & Bruce, 1988) found patterns of results that could be best described as a linear effect of orientation.

The difference as such appears systematic and demands an explanation. One possibility is that the use of reaction time versus accuracy as the dependent measure is the key factor. It is well known that reaction times are related to stimulus contrast through a compressive power function (Pieron, 1920). A similar nonlinear, compressive transformation could linearize the dependence of reaction time on rotation by acting on an internal representation of "face contrast" having an opposite convexity (an immediate analogy is linearization of luminance in a CRT monitor by gamma correction). Even if the linearization is not perfect, the nonlinear trend might be reduced to the point of being below the threshold of statistical significance. Other behavioral tasks, not involving the measurement of time to response but rather a more qualitative judgment, like the one investigated here, might instead function in a different way, being more directly dependent on the strength and quality of the response to faces.

Another possible explanation concerns the extent to which the stimulus/task combination emphasizes the "holistic", at the expense of the "part-based" component of face processing. It has been argued by many authors (Leder & Bruce, 1998; McKone et al., 2001; Moscovitch et al., 1997) that upright faces receive both holistic and part-based processing. Of the studies that have found nonlinear orientation effects, most (present study, McKone, 2004; McKone et al., 2001; Moscovitch et al., 1997) have used methods that are likely to emphasize the holistic component, demonstrating that the phenomenon of interest occurs for whole faces, but not for isolated face parts or for scrambled faces; in addition, (Murray et al., 2000) used a method based on the Thatcher illusion, which placed the orientation of the whole face and of local parts in opposition to one another. In contrast, those studies that have found linear orientation effects have used methods that were unlikely to dissociate holistic and part-based contributions, and thus may have produced orientation effects that were based on a combination of the two influences. Under this view, it would be the holistic coding strategy that would produce the Gaussian orientation tuning function reported here.

4.2. Interpretation of orientation tuning

Single unit recordings from temporal visual areas in primates have revealed the existence of neurons that are tuned to a limited range of views of a novel object (Logothetis, Pauls, & Poggio, 1995). Similarly, neurons in inferotemporal cortex of monkeys were found to respond selectively to a limited range of views of a head or body (Ashbridge, Perrett, Oram, & Jellema, 2000; Perrett, Oram, & Ashbridge, 1998). The presence of these neurons fits well with computational theories of object recognition that are based on the ensemble response of a population of mechanisms narrowly tuned to a specific view of an object. Such recognition schemes are based on small metric transformations of the object followed by matching to a limited number of learned views stored in memory (Bricolo, Poggio, & Logothetis, 1996; Logothetis, Pauls, Bulthoff, & Poggio, 1994; Poggio & Edelman, 1990; Ullman, 1996). We consider here only mechanisms tuned to different orientations of the face in the image plane. In monkeys, the individual orientation preferences of these face/body-selective neurons have been found distributed across all orientations, but with a prevalence of units tuned to the upright view (Ashbridge et al., 2000). Because of the greater number of such upright-tuned mechanisms, the overall population response is not orientation-invariant, but instead shows a preferential tuning centered on the upright view. The orientation bandwidth of single neurons, as well as that of the population as a whole, was found to be approximately 90 deg. Interestingly, the orientation bandwidth of approximately 90 deg that we have estimated for humans is close to the tuning recovered for several image characteristics from neurophysiological recordings in several extrastriate areas of monkey cortex, including body orientation in the image plane (Ashbridge et al., 2000), angle of view of the head (Perrett et al., 1991), sensitivity to the direction of motion of objects (Oram, Perrett, & Hietanen, 1993) and of stochastic stimuli (Britten & Newsome, 1998).

These neurophysiological findings inspire our interpretation of the observers' responses in our task. Assume that the strength of the percept of a face at a given orientation is proportional to the linear combination of the activity of all the units that are sensitive to that view. If upright-selective units are more numerous, an upright face of low contrast might be able to evoke a larger response than an inverted face with higher contrast, because it will recruit a larger number of units. If all units have similar tuning bandwidth and populate densely the orientation spectrum, then the population response will be centered on upright and will appear to have a bandwidth equivalent to that of the average single unit and a magnitude proportional to the imbalance in the number of units sensitive to different views. Unfortunately, we have no means of measuring psychophysically the direct correlate of such activity. However, we can use an indirect method based on matching, where we measure the strength needed to equalize the percepts of a test stimulus at several orientations relative to a fixed template. Our stimuli are transparent and rivalrous, so our situation is similar to that encountered with certain motion plaids, where two sets of dots moving in different directions are seen as transparent surfaces sliding past each other, rather than a single, coherent surface moving along the vector-average direction of motion (Treue, Hol, & Rauber, 2000). If the difference in orientation between the two faces is greater than the bandwidth of the tuning functions, then the population response will have two peaks of activity. These two population peaks could compete with each other for perceptual dominance and depending on the relative numerosity of the underlying units, one stimulus orientation might be more salient and prevail more often, explaining the pattern of results obtained. However, as in the motion case, transparency and perceptual dominance is observed also for orientation differences smaller than the tuning bandwidth, so that multi-peaked population profiles cannot be the explanation. Rather, a more selective reading of the responses of individual units seems necessary. This raises the possibility that the pattern of results observed might derive from selective pooling of information from a small set of units with higher sensitivity, rather than the unselective pooling of activity from a population with anisotropic distribution of orientation preferences. Similar arguments have recently been put forward to explain the correlation between activity in MT neurons and perceptual decisions in motion direction discrimination tasks (Purushothaman & Bradley, 2005). Thus, this account proposes that upright tuned units are more sensitive than units tuned to other orientations, leading to the advantage demonstrated in the present experiments.

4.3. Role of the facial configuration

The observers' responses to images where the normal configuration of the features in the face was disrupted (experiment 2) have revealed no anisotropies in orientation preference. Here, the scrambling operation forces the recognition system to operate at a lower level of categorization, since the jumbled features no longer qualify as a face. It appears that at this level of analysis all feature orientations evoke responses of identical magnitude. View-dependent models of recognition assume that a limited number of views are stored in memory following exposure to the stimulus: the prevalence of mechanisms sensitive to a particular orientation is then taken to reflect the greater exposure afforded to such canonical stimulus orientation. Given that facial features, as well as the whole face, are experienced more often in the canonical upright view, the lack of any selective advantage for upright features found in our experiment is interesting, in that it is troubling for accounts that explain the upright-face advantage as simply induced by expertise and dependent on upright detectors being more numerous in the population (Diamond & Carey, 1986).

While it is certainly possible that upright tuned units are more numerous in the neural population, we favor the hypothesis that the results obtained in our experiments reflect the activity of mechanisms tuned to the upright orientation and with higher sensitivity, forming a specialized subclass of face-selective, configuration dependent recognition units.

Acknowledgments

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