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Gaze constancy in upright and inverted faces.

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The dual-route model (Otsuka, Mareschal, Calder, & Clifford, 2014) posits that constancy in the perception of gaze direction across lateral head rotation depends on the integration of information from the eye region and information about head rotation. Incorporation of information about head rotation serves to compensate for the change in eye-region information when viewing a rotated head. We tested the ability of this model to predict the magnitude of Wollaston's effect: When eyes from a frontal pose are inserted into an angled face, the perceived direction of gaze appears attracted towards the direction of the head. The framework of the dual-route model explains Wollaston's effect as a result of the misapplication of this same integration operation without any change in eye-region information. To test this explanation, we compared the magnitude of the integration occurring for Wollaston's effect to that for normal faces. Here, participants performed categorical judgment of gaze direction across head rotation poses in three image conditions: normal face, eyes-only, and Wollaston. Integration of eye and head information was inferred by comparing the effect of pose between the eyes-only condition and the normal face condition, and by examining the effect of pose in the Wollaston condition. Consistent with the dual-route model, the magnitude of integration was similar between the normal face condition and the Wollaston condition. Further, upright and inverted faces yielded similar levels of gaze constancy, showing that the dual-route model applies to the perception of gaze direction in inverted faces as well as in upright faces.

Introduction

Perceptual constancy denotes our ability to see invariant properties of objects such as size, shape, or lightness despite changes in the retinal image. In this paper, we consider perception of another's gaze direction across various head rotations as a case of perceptual constancy. For the special case of a frontally oriented face, the gaze direction can be discerned simply by the relative position of iris and pupil in the eyes (left position: leftward gaze; central position: direct gaze; rightward position: right gaze). However, direct gaze toward the observer can also be expressed as a leftward position of iris and pupil in a rightward-oriented face and vice versa. Despite such changes in image configuration expressing the direction of gaze across head rotation, we can perceive gaze direction relatively accurately and consistently without any noticeable difficulty. Here, we call this ability "gaze constancy" (Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011; Gibson & Pick, 1963; Todorovic, 2006). Many previous studies have reported that gaze constancy is not a perfect constancy, but that the perceived gaze direction is slightly biased in the opposite direction to the head rotation (repulsive effect: Anstis, Mayhew, & Morley, 1969; Gamer & Hecht, 2007; Gibson & Pick, 1963; Masame, 1990; Noll, 1976).

In our recent study (Otsuka, Mareschal, Calder, & Clifford, 2014), we measured the effect of head rotation on the perceived gaze direction in an eye-region condition, in which little or no information about head rotation is available, as well as in a whole-head condition, in which the head is fully visible. We found the repulsive effect of head rotation was most pronounced in the Eye-region condition (only a

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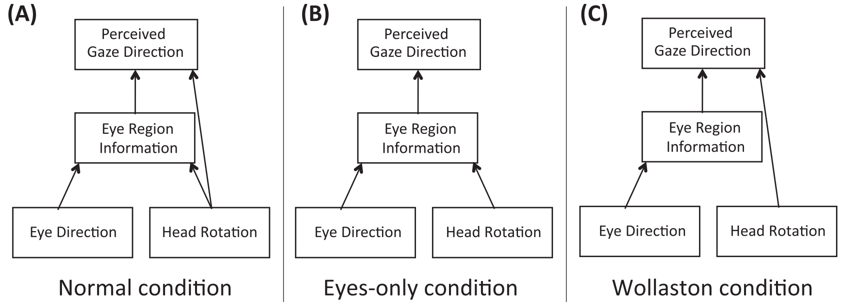

Figure 1. Schematic of the dual-route model (Otsuka et al., 2014) as applied to each of the three different conditions. (A) The influence of head rotation in the Normal condition involves two distinct routes: as an indirect cue via the change in eye-region information, and as a direct cue via head rotation. (B) The influence of head rotation in the Eyes-only condition is limited to an indirect cue via the change in eye-region information. (C) The influence of head rotation in the Wollaston condition is exclusively as a direct cue.

rectangular region around the eyes was visible, including the bridge of the nose). By contrast, the perceived gaze direction was mostly constant in the Whole-head condition. In the Eye-region condition, the proportion of "direct" gaze responses to stimuli with physically direct gaze when faces rotated laterally by $\pm 30°$ was reduced to 52.9% ($SD = 25.4$), the proportion of "direct" responses for frontal face angle (0°). By contrast, the proportion of such veridical "direct" gaze responses with the rotated face remained at 76.9% ($SD = 37.8$) of that for the frontal face in the Whole-face condition. Based on such observations, we developed a dual-route model of the effect of head rotation on perceived gaze direction.

In the framework of the dual-route model, we described the effect of head rotation on perceived gaze direction as normally involving two distinct routes. These two routes correspond to the two arrows from head rotation in the schematic of the dual-route model (Figure 1A). First, changes in the visible part of the eye on either side of the iris as the head rotates induce the repulsive effect (Anstis et al., 1969; Gamer & Hecht, 2007; Gibson & Pick, 1963; Masame, 1990; Noll, 1976). For example, as the head rotates to the right with gaze fixed on a given point (e.g., directly ahead), the relative amount of visible white (sclera) on the right side of the iris increases, just as when eye direction shifts toward the left. Such a change biases the perceived gaze direction in the opposite direction to head rotation (repulsive effect). In the schematic (Figure 1A), the repulsive effect is illustrated as the arrow from head rotation to eye-region information, suggesting that head rotation acts as an indirect cue for the perceived gaze direction via the change in eye-region information. Second, information about head rotation acts as a direct cue for gaze direction that attracts the perceived gaze direction toward the head rotation (attractive effect) and tends to compensate for bias occurring through the former effect. This latter route of the effect of head rotation is illustrated by the direct arrow from head rotation to perceived gaze direction in the schematic (Figure 1A). Our results and the framework of the dual-route model suggest that gaze constancy depends on the latter process that integrates information from the eyes with information about head rotation. When the visible facial area is confined to a small area around eyes, the influence of head rotation is limited to an indirect cue via the change in eye-region information (Figure 1B), hence resulting in a pronounced repulsive effect (Otsuka et al., 2014).

In our previous study (Otsuka et al., 2014), we also proposed that operation of the direct cue is consistent with the observation of Wollaston's effect. Wollaston's effect refers to the shift in the perceived gaze direction from identical eyes depending on the head rotation context, as first demonstrated by Wollaston (1824). Wollaston's demonstration depicts two differentially angled faces in which identical eyes are inserted. Typically, the perceived gaze direction of the eyes is attracted towards the head rotation context (Langton, Honeyman, & Tessler, 2004; Maruyama & Endo, 1983; Todorovic, 2006, 2009). The dramatic shift of perceived gaze direction from identical eyes depending on the facial rotation context in Wollaston's demonstration has led several researchers to describe this effect as a perceptual illusion (Langton et al., 2004; Nakato et al., 2009; Tomonaga & Imura, 2010; but also see Todorovic, 2006). However, the framework of the dual-route model suggests that Wollaston's effect can be described as an example of over-constancy through the misapplication of a process that normally maintains gaze constancy in spite of changes in the visible part of the eyes with head rotation. As the use of identical eyes eliminates any indirect influence of head rotation (i.e., the change in the visible part of the eyes that induces the repulsive effect), the influence of head rotation in this case is exclusive to the direct cue that induces the attractive effect (Figure 1C). In this way, the operation of the direct cue that integrates information from the eye region with information about head rotation produces the pronounced attractive effect seen in Wollaston's demonstration.

In summary, the dual-route model posits that the operation of a single, direct cue that integrates information from the eyes with information about head rotation underlies both the improved gaze constancy in viewing the whole face and Wollaston's effect. This led us to hypothesize that the direct influence of head rotation on perceived gaze direction as found in Wollaston's effect would be similar to that found for normal faces.

In order to test and validate the dual-route model, the current study examined the integration of information from the eyes with head rotation in two ways. First, we examined the difference in the effect of head rotation between the Eyes-only condition and the Normal face condition as in our previous study (Otsuka et al., 2014). In line with our previous results, we expected that the repulsive bias would be reduced in the Normal condition relative to the Eyes-only condition. The degree of reduction of the repulsive bias indicates the magnitude of integration between eyes and head rotation information in the Normal condition. Second, we examined the strength of the effect of head rotation in the Wollaston condition based on the demonstration by Wollaston (1824), where eyes from a frontal pose were inserted into an angled face. The magnitude of the effect of face rotation context on the perceived gaze direction from identical eyes indicates the relative weighting with which information from the eye region is integrated with information about head rotation in the Wollaston condition. The framework of the dual-route model predicts that the magnitude of integration measured would be similar between the Normal condition and Wollaston condition.

Further, in order to elucidate the nature of the integration of information from the eyes with head rotation information in gaze processing, we introduced an image inversion manipulation. Many previous studies have reported that inverted faces are difficult to recognize (e.g., Yin, 1969). Such difficulty is thought to occur because facial inversion disrupts our ability to integrate information across facial features (e.g., Young, Hellawell, & Hay, 1987). In the current study, we tested whether facial inversion influences gaze constancy by affecting the integration of information from the eyes with information about head rotation.

Experiment

Methods

Participants

Twenty naïve observers (ten male and ten female) served as subjects (mean age = 19.05 years; $SD = 2.65$ years). Data from one female subject was removed from analysis because this subject made "direct" response in 80% of the trials. All had normal or corrected-to-normal vision. All experiments adhered to the declaration of Helsinki guidelines and were approved by the UNSW Human Research Ethics Committee.

Apparatus

A Dell Z220 Work Station computer running Matlab™ (MathWorks Ltd) was used for stimulus generation, experiment control and recording subjects' responses. The programs controlling the experiment incorporated elements of the PsychToolbox (Brainard, 1997). Stimuli were displayed on a Viewsonic Graphics Series G90f (1024 × 768 pixels) driven by an NVIDIA Gigabyte GeForce GTX 750 Ti graphics card. The display was calibrated using a photometer and linearized using look-up tables in software.

Stimuli

Four grey-scale synthetic neutral faces (two male faces and two female faces) were created using FaceGen Modeller 3.5. The 3d models of faces created in FaceGen were imported into Blender 2.70. The original eyes in the faces were replaced with 3d model eyes created in Blender. Each eye was set to track a fixation target using the "AutoTrack" feature in Blender. The deviation of each eye was controlled by changing the angular position of the fixation target in the horizontal plane.

There were three image conditions: Normal condition, Eyes-only condition, and Wollaston condition (Figure 2). Images for the Normal condition were the ones originally rendered in Blender. In the Eyes-only condition, facial images were masked except for the region around each eye. The contours of the mask had the same shape as the outer contours of the exposed area of the eyes. The images for the Wollaston condition were created by inserting the eyes (and some of the surrounding area) of the frontal face (0° pose) into the rightward angled face (20° pose). In addition to the lateral 20° rotation, the angled faces were rotated clockwise by 3° of roll in the frontal plane of the face. All images were rendered with the camera pointed at the right eye of each face. These settings ensured the optimal fitting of the eyes of the frontal faces into the angled faces without any rotation of the eyes or change in the distance between the eyes. A single light source from above the camera illuminated the faces. For all image conditions, the images with leftward angled pose (–20° pose) were created by left-right reversing the images with rightward angled pose. Left-right reversed versions were created also for the images with frontal

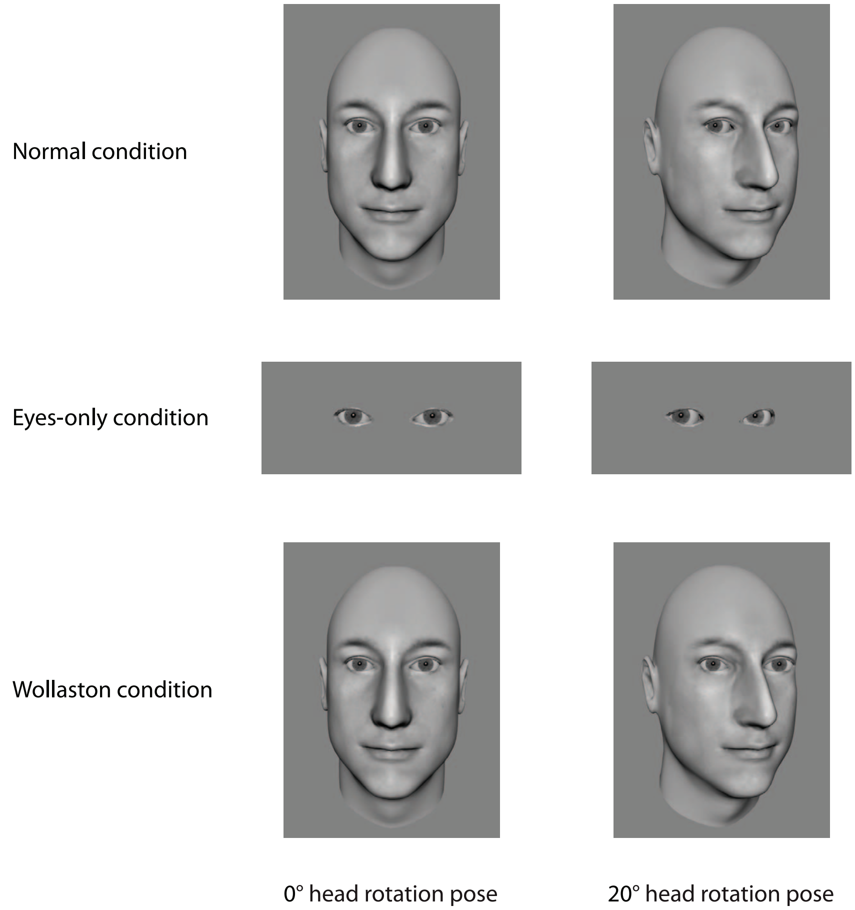

Figure 2. Example stimuli in each condition showing 0° eye deviation in the upright image orientation. Images in the Wollaston condition were created by inserting the eyes in the Normal condition with 0° head rotation pose into the angled head. Thus, images in the 0° head rotation pose for Wollaston condition were identical to those for the Normal condition.

pose. For each subject, two of the faces were shown using the original images in frontal pose, and the other two faces were shown using the left-right reversed version. Inverted versions of the stimuli were created by flipping each image vertically.

The faces subtended $19° \times 11°$ of visual angle on average and were viewed at 57 cm in a dimly lit room. All images were shown against a medium grey background. Examples of the stimuli in each condition are shown in Figure 2.

Procedure

The observers' task was to indicate whether the direction of gaze was averted to the left, direct, or averted to the right using key-presses "Left Arrow," "Down Arrow" and "Right Arrow," respectively. They were given the following verbal instructions; "On each trial, you will be shown either an image of a face, or of eyes only. Your task is to judge the gaze direction, whether it is looking to YOUR LEFT, looking STRAIGHT AT YOU, or looking to YOUR RIGHT." Each stimulus was presented in a raised cosine temporal window, such that ramping on and off took 200 ms each (total duration of 400 ms), followed by a grey screen until a response was recorded. This temporal windowing procedure was applied to reduce the discomfort of onset and offset of a large image for the observer and to abolish temporal transients. On each trial, stimulus position was randomly jittered horizontally and vertically $\pm 0.83°$ of visual angle around the center of the screen in order to ensure that subjects were responding to global stimulus configuration rather than adopting a strategy of attending to a particular part of the screen. The next trial was initiated 600 ms after a response was made.

Each subject completed a total of 1728 trials consisting of 16 blocks of 108 trials. Stimuli for each pose, condition, and image orientation were shown in separate blocks. In each block, stimuli were presented in a random order with 4 facial identity $\times$ 9 different eye deviations (–20°, –15°, –10°, –5°, 0°, 5°, 10°, 15°, 20°) $\times$ 3 repetitions. Note, we use the term "eye deviation" to refer to the physical direction of the eyes relative to the observer. We reserve the term "gaze direction" for the subjective percept. As the stimuli

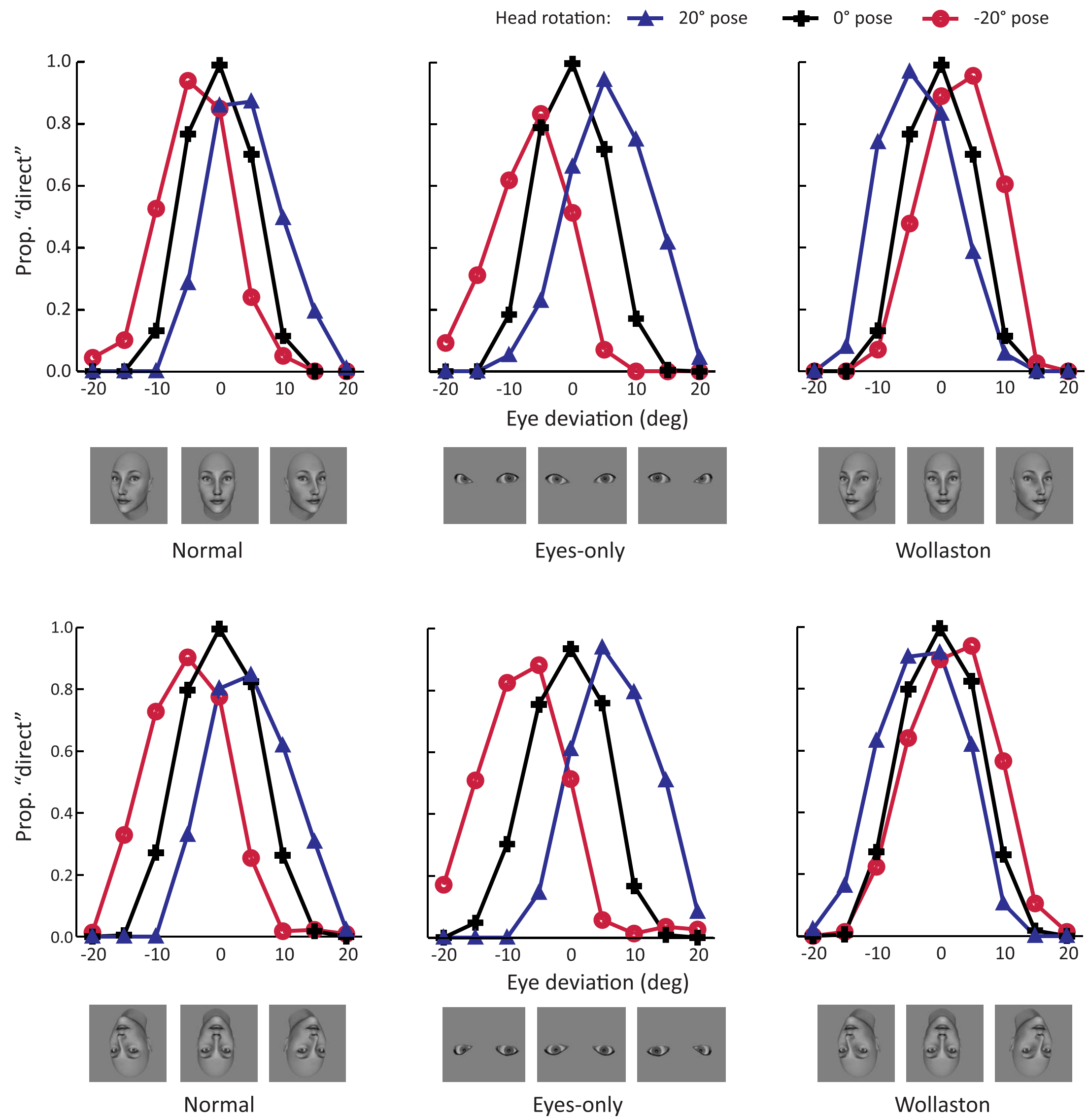

Figure 3. Averaged proportion of direct responses as a function of eye deviation for each head rotation and condition. The graphs on the top show results from upright images, and those on the bottom show results from inverted images.

with 0° head rotation were identical between the Normal and Wollaston condition, only one set of data was collected. Identical data were then used for the analysis in both conditions.

Analysis

Subjects' reports of direction of gaze as leftwards, direct, or rightwards were recoded as follows: leftward = 0; direct = 0.5; rightwards = 1. For each condition, pose, and image orientation, a proportion rightwards score for presentations of each eye deviation was calculated as the sum of recoded scores divided by the number of presentations. The following analysis was performed both on the data averaged across subjects (results shown in Figures 3 through 5) and on the individual data (results shown in Figures 6 and 7).

For each head rotation pose in each condition and image orientation, the proportion rightwards score was fitted as a logistic function of eye deviation (Figure 4). The 50% point of each resulting psychometric function was taken as the eye deviation corresponding to subjectively direct gaze. On these points we performed linear regression as a function of the degree of head rotation pose (Figure 5). The slope of the regression line, m, was used to estimate the degree of gaze constancy, quantified by a constancy index. Hence, $m = 0$ corresponds to no effect of head rotation, $m > 0$ to a repulsive effect of head rotation, and $m < 0$ to an attractive effect of head rotation. The gaze constancy index was calculated by subtracting m from 1 (Figure 6).

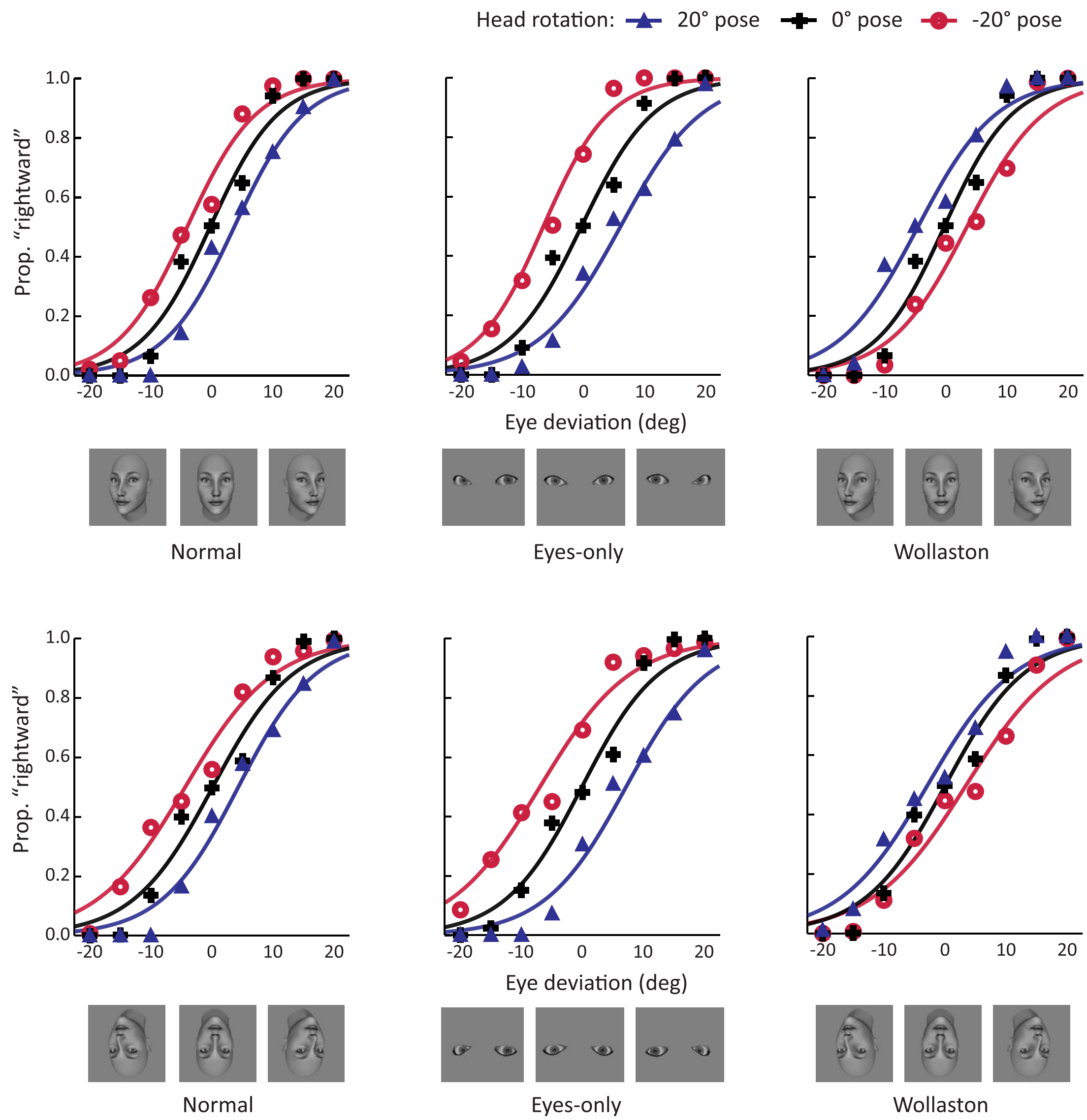

Figure 4. Logistic fits to the averaged data recoded as the proportion of rightwards responses. The graphs on the top show results from upright images, and those on the bottom shows results from inverted images.

The slope of the regression line, m, was also used to estimate the relative weighting of eye deviation, E, and head rotation, H, in determining perceived direction of gaze, G. The perceived direction of gaze was modelled as a weighted average of the eye deviation and head rotation, such that two weights were constrained to sum to one:

$$G = \left(\frac{1}{1-m}\right)E + \left(\frac{m}{m-1}\right)H. \quad (1)$$

For example, if the slope of the regression line was $m = 0$, corresponding to no effect of head rotation, then the weightings attached to eye deviation and head rotation would be one and zero respectively, such that perceived direction of gaze would simply be equal to the eye deviation. If, instead, the slope of the regression line was $m = -1$, eye deviation and head rotation would be combined, with each given a weighting of 0.5.

Pairs of weights were derived separately for the Normal, Eyes-only, and Wollaston conditions.

As shown in the schematics of the dual-route model as applied to each condition (Figure 1), the influence of head rotation in the Normal condition involves two distinct routes: an indirect cue via the change in eye-region information, and a direct cue via head rotation. On the other hand, the Eyes-only condition involves only the indirect cue and the Wollaston condition involves only the direct cue. Thus, the estimated weighting of head rotation (H) for the Eyes-only condition and that for the Wollaston condition were reported as the weighting of the indirect cue (Figure 7B) and the weighting of direct cue (Figure 7A), respectively.

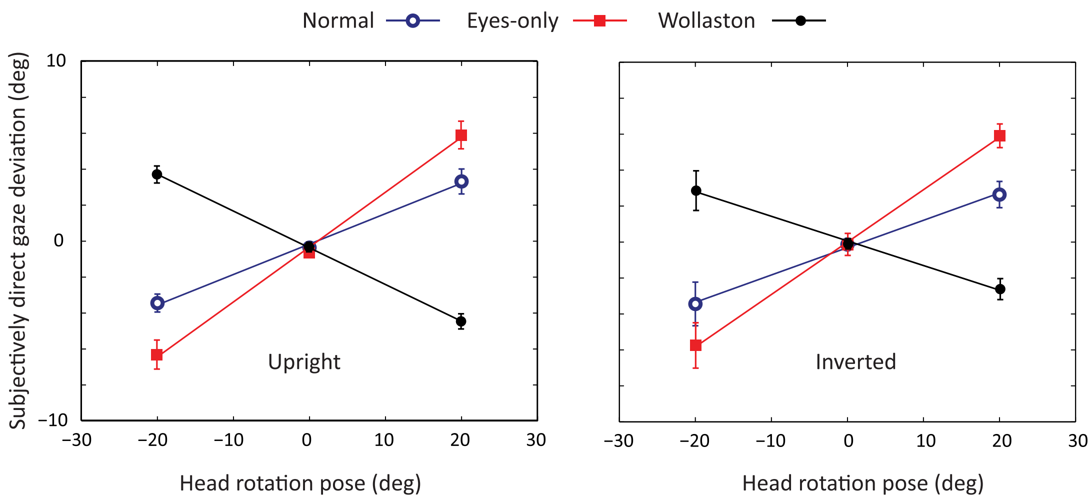

Figure 5. Points of subjectively direct gaze derived from the logistic fitted data. Solid lines are best fitting linear regression across head rotation for each condition, in the upright images (left) and in the inverted images (right). Error bars represent ±1 standard deviation between subjects.

For the Normal condition, the contributions of eye deviation and head rotation to perceived direction of gaze, G_{NORMAL}, were decomposed into a weighted combination of information from the eyes (Eyes-only condition), $G_{EYES\text{-}ONLY}$, and the effect of head rotation as a direct influence on perceived direction of gaze according to the following equation:

$$G_{NORMAL} = \left(\frac{1 - m_{EYES\text{-}ONLY}}{1 - m_{NORMAL}}\right) G_{EYES\text{-}ONLY} + \left(\frac{m_{NORMAL} - m_{EYES\text{-}ONLY}}{m_{NORMAL} - 1}\right) H, \quad (2)$$

where m_{NORMAL} and $m_{EYES\text{-}ONLY}$ are the slopes of the regression lines from the Normal and Eyes-only conditions, respectively (for a derivation of Equation 2, please see Appendix). For the Normal condition, this latter estimate of the weighting on H was reported as the weighting of head rotation as a direct cue (Figure 7A).

Results

Figure 3 shows the averaged proportion of "direct" responses as a function of eye deviation for each head rotation and condition. Figure 4 shows the logistic fits to the data recoded as the proportion of the rightwards responses for each combination of head rotation and condition. Both Figures 3 and 4 show the same general pattern of results between the upright and inverted image orientations with the opposite (attractive) effect of head rotation for the Wollaston condition compared to the repulsive effect evident in the other two conditions.

The eye deviation eliciting the 50% proportion rightwards response from each psychometric function in Figure 4 corresponds to the point of subjectively direct gaze for each head rotation. Figure 5 shows the points of subjectively direct gaze together with the linear regression fits across head rotation pose in the upright and inverted images. For both upright and inverted image orientations, the psychometric functions and the points of subjectively direct gaze shift opposite to the direction of head rotation for the Wollaston condition. On the other hand, they shift toward the direction of head rotation for the Normal condition and Eyes-only condition, and to a greater extent for the Eyes-only condition. These results indicate that the perceived direction of gaze is repelled from the rotation of the head in the Normal condition and Eyes-only condition, whereas it is attracted toward the head rotation in the Wollaston condition.

To quantify the degree of gaze constancy over head rotation in each condition, we calculated a gaze constancy index by subtracting the slopes of the linear regression fits to subjectively direct gaze across head rotation pose (Figure 4) from 1. A constancy index of 1 indicates perfect constancy (no effect of head rotation on perceived gaze direction, or veridical gaze perception despite variation in eye region information and head rotation, corresponding to slope = 0), an index of 0 indicates no constancy (eye deviation relative to head rotation as the sole determinant of the perceived gaze direction, corresponding to slope = 1), and an index above 1 indicates overconstancy (overall attractive influence of head rotation on the perceived gaze direction, corresponding to slope < 0).

The Box plots depicting the gaze constancy index (Figure 6) suggest partial constancy for the Normal condition and Eyes-only condition across image

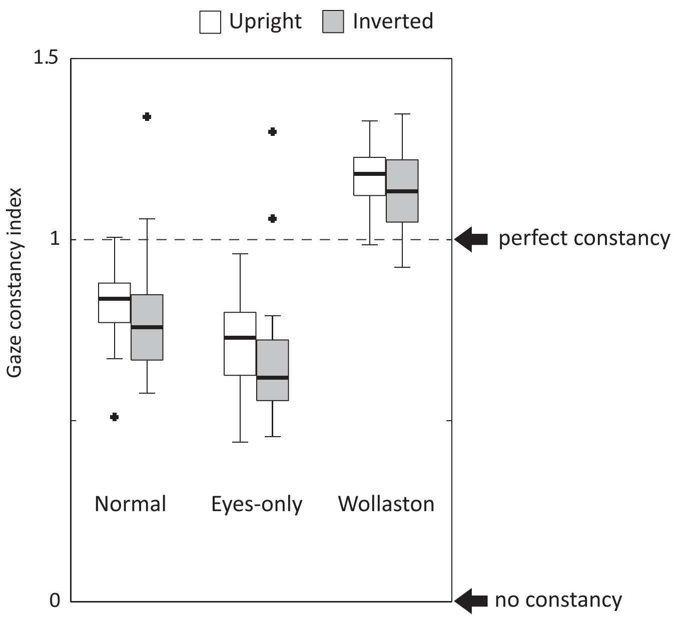

Figure 6. Box plot summarizing the individual gaze constancy index for each condition in the upright and inverted image orientation. A constancy index of 1 indicates perfect constancy, an index of 0 indicates no constancy, and an index above 1 indicates overconstancy. The whiskers represent the most extreme data value within 1.5 times the inter-quartile range. Outlier values are depicted as +.

orientations, while it suggests overconstancy for the Wollaston condition. As the data departed from normality, we performed nonparametric tests. One-sample Wilcoxon Signed-Rank Tests using a Holm-Bonferroni correction showed that all index values significantly differed from a perfect constancy value of one (Upright Normal: $p < 0.01$, $d = 1.59$; Upright Eyes-only: $p < 0.01$, $d = 2.05$; Upright Wollaston: $p < 0.01$, $d = 1.96$; Inverted Normal: $p < 0.01$, $d = 1.13$; Inverted Eyes-only: $p < 0.01$, $d = 1.60$; Inverted Wollaston: $p < 0.01$, $d = 1.21$). A Friedman's analysis of variance was performed to examine differences between the conditions and image orientations. The analysis revealed significant variation in the constancy index, χ^2 (5, $N = 19$) = 76.26, $p < 0.01$. Wilcoxon Signed-Rank Tests using a Holm-Bonferroni correction comparing the constancy index between the upright and inverted images showed no significant difference in either of the conditions (ps > 0.1). On the other hand, Wilcoxon Signed-Rank Tests using a Holm-Bonferroni correction comparing the constancy index between the conditions revealed that the constancy indices for the Wollaston condition were significantly greater than those for the Normal condition in both upright and inverted image orientations (Upright: $p < 0.01$, $d = 3.34$; Inverted: $p < 0.01$, $d = 2.18$). The analysis further revealed that the constancy indices for the Normal condition were significantly greater than those for the Eyes-only condition in both upright and inverted image orientations (Upright: $p < 0.01$, $d = 0.85$; Inverted: $p < 0.01$, $d = 0.63$). These results suggest a similar degree of gaze constancy across upright and inverted image orientations, and demonstrate improved gaze constancy in the Normal condition compared to the Eyes-only condition across image orientations.

Importantly, the regression slope for the Normal condition is shallower compared to the Eyes-only condition (Figure 5), indicating that the repulsive effect is reduced in the Normal condition. As the Normal condition and Eyes-only condition share identical eyes, the shallower regression slope for the Normal condition demonstrates integration between eyes and head rotation information in such a way that the attractive effect of the head rotation reduces the overall repulsive effect. As the Wollaston condition shares the identical eyes across head rotation, the influence of head rotation itself indicates the degree of integration in this condition. In order to compare the magnitude of the integration effect between the conditions and between image orientations, we calculated the relative weighting of the information from the eyes and the head rotation in determining the direction of gaze perception in each condition from the slopes of the regression lines for each observer. Based on the dual-route model (Otsuka et al., 2014), we estimated the weighting of head rotation as a direct cue that reflects the integration between eyes and head rotation information.

Figure 7A shows Box plots depicting the weighting of head rotation as a direct cue for the Normal condition and for the Wollaston condition in each image orientation calculated for each observer. The weightings for Normal conditions were calculated based on the slopes of the regression lines from the Normal and Eyes-only conditions, while those for the Wollaston condition were based on the slope of Wollaston condition alone. The weightings of head rotation as a direct cue are generally greater than zero, corresponding to an attractive influence of head rotation. As the data are skewed, we performed one-sample Wilcoxon Signed-Rank Tests using a Holm-Bonferroni correction to compare the weightings against zero. The analysis showed that the weighting of the direct cue was significantly above zero across the conditions and image orientations (upright Normal: $p < 0.01$, $d = 1.07$; upright Wollaston: $p < 0.01$, $d = 2.15$; inverted Normal: $p < 0.01$, $d = 1.22$; inverted Wollaston: $p < 0.01$, $d = 1.26$). Friedman's analysis of variance revealed no significant difference between the conditions ($p = 0.11$), suggesting a similar level of integration effect across conditions and image orientations. In addition, the weightings of the indirect head rotation cue for the Eyes-only condition (Figure 7B) were generally negative, suggesting a repulsive influence of head rotation. A Wilcoxon Signed-Rank Test

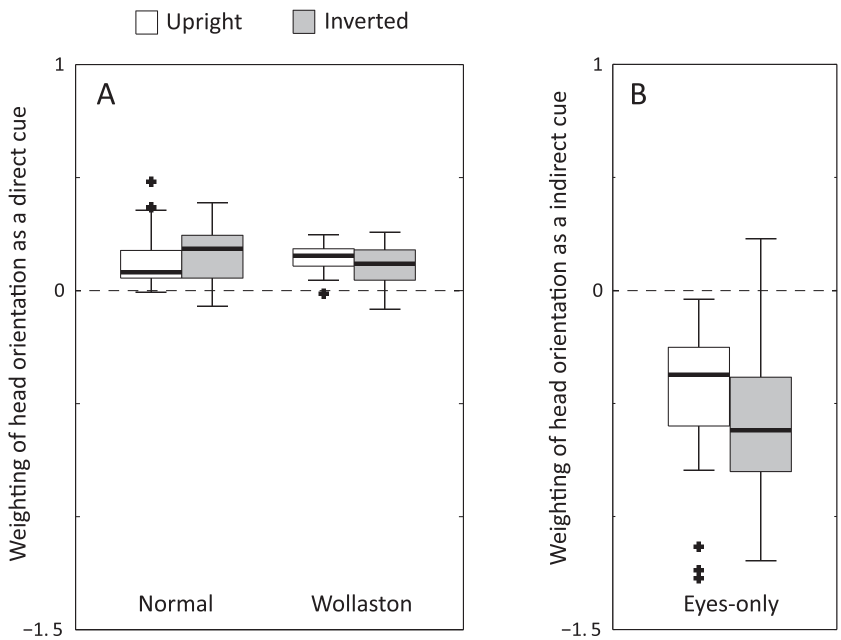

Figure 7. Box plots summarizing individual subjects' ($n = 19$) weighting of head rotation in the upright and inverted image orientations. Weighting of head rotation as a direct cue in the Normal conditions and Wollaston condition (A), and weighting of head rotation as an indirect cue estimated from the data of the Eyes-only condition (B). The box covers the interquartile range, and the median is indicated by the mark within the box. The whiskers represent the most extreme data value within 1.5 times the interquartile range. Outlier values are depicted as +.

revealed no significant difference between the weightings in the upright and inverted image orientations (*p*s $= 0.18$). The results suggest that the repulsive as well as the attractive influence of head rotation were similar between upright and inverted image orientations.

As the direction of gaze is defined along a physical continuum, we chose to use the 50% point of the fitted (logistic) psychometric function as our measure of the direction of subjectively direct gaze as reported above. In alternative analyses (not shown), we found a consistent pattern of results using (a) the centroid of "direct gaze" response and (b) the "peak of direct gaze" estimated by fitting separate logistic functions to the proportion of "left" and "right" responses, as described in previous studies (Ewbank, Jennings, & Calder, 2009; Mareschal, Calder, Dadds, et al., 2013; Stoyanova, Ewbank & Calder, 2010; Vida & Maurer, 2012). This consistency confirms the robustness of the result to the precise method employed to estimate subjectively direct gaze.

Although we did not find any effect of facial inversion on the integration of information about eyes and head rotation, we found facial inversion had some influence on participants' gaze judgment performance. Figure 8 shows Box plots depicting the proportion of "direct" response across eye deviation for each head rotation pose and condition in the upright and inverted image orientation. Across conditions and head rotation pose, there was a tendency for the proportion of "direct" responses to increase for the inverted orientation. A three-way repeated ANOVA with head rotation pose (–20°/0°/20°), condition (Normal/Eyes-only/Wollaston), and image orientation (upright/inverted) confirmed this tendency by showing a marginally significant main effect of image orientation, $F(1, 18) = 4.07$, $p = 0.06$, $\eta_p^2 = 0.18$. In addition, there was a main effect of condition, $F(2, 36) = 9.68$, $p < 0.01$, $\eta_p^2 = 0.35$, which interacted with head rotation pose, $F(4, 72) = 3.92$, $p < 0.01$, $\eta_p^2 = 0.18$. Post hoc analysis using a Holm-Bonferroni correction showed that at –20° pose, the proportion of "direct" response was significantly greater in the Wollaston condition compared to the other two conditions (*p*s < 0.05), and that at 20° pose it was significantly smaller in Normal condition compared to the other two conditions (*p*s < 0.05).

In alternative analyses (not shown), we found the same pattern of results using the width of the cone of "direct" gaze estimated by fitting separate logistic functions to the proportion of "left" and "right" responses, as described in previous studies (Ewbank et al., 2009; Mareschal, Calder, Dadds et al., 2013; Stoyanova et al., 2010; Vida & Maurer, 2012).

Discussion

We found that the integration of information from the eyes with head rotation information was similar

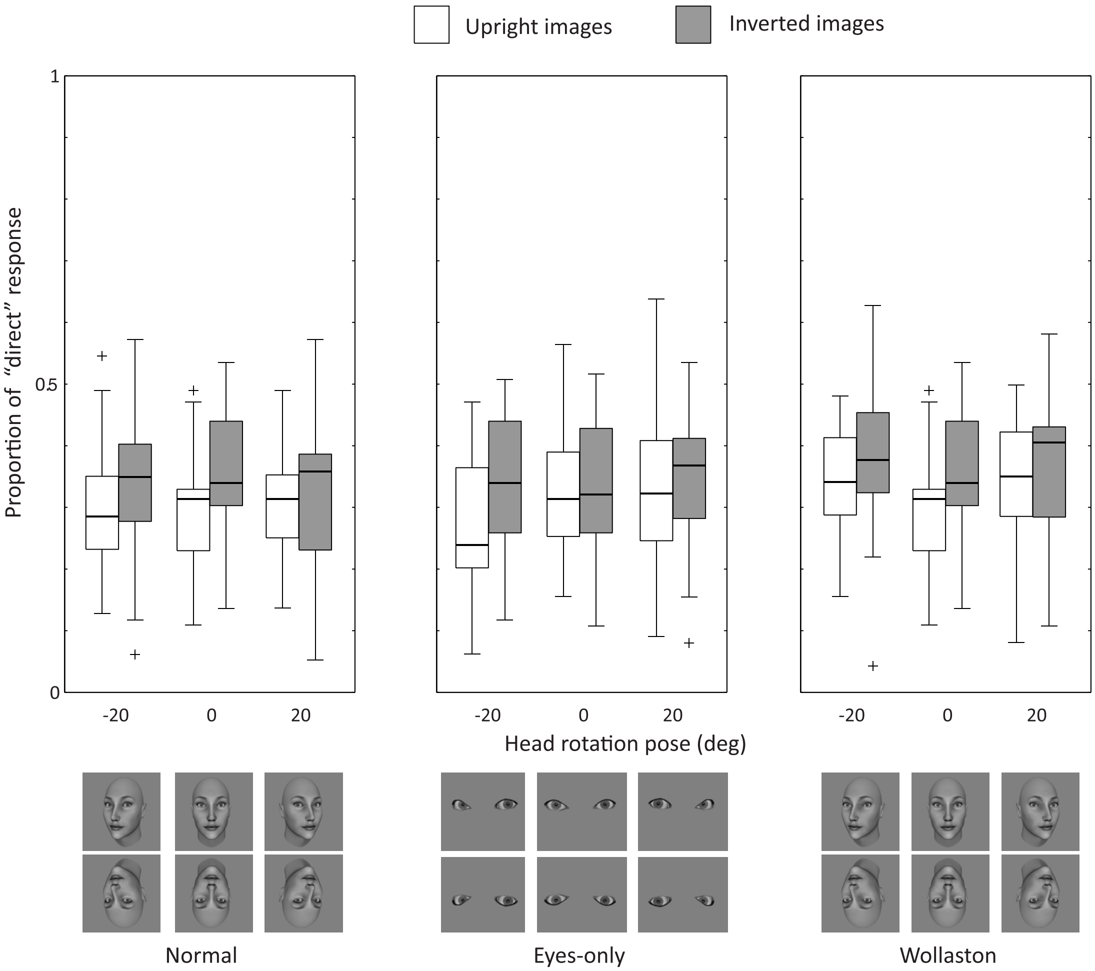

Figure 8. Box plot summarizing the proportion of "direct" responses across eye deviation for each head rotation pose and condition in the upright and inverted image orientation. The whiskers represent the most extreme data value within 1.5 times the interquartile range. Outlier values are depicted as +.

between the Normal and Wollaston conditions regardless of the upright or inverted orientation of the images. Consistent with our previous study (Otsuka et al., 2014), the repulsive effect of head rotation on the perceived gaze direction was more pronounced when only the eyes were visible (Eyes-only condition) compared to when the whole face was visible (Normal condition). Such a reduction of the repulsive effect suggests that the visual system compensates for biased information obtained from the angled eyes by integrating information about head rotation with information from the eye region. Values of the gaze constancy index were similar between upright and inverted orientations, with a higher value for the Normal condition ($M = 0.80$, $SD = 0.14$) than the Eyes-only condition ($M = 0.68$, $SD = 0.16$) across image orientations. The results thus demonstrate improved gaze constancy in the Normal condition compared to the Eyes-only condition.

The average weighting of 0.14 ($SD = 0.13$) for the direct head cue in the upright Normal condition found in the current study is similar to the corresponding average weighting value of 0.13($SD = 0.11$) we found in our previous study (Otsuka et al., 2014). Further, we found that the strength of integration between head and eyes was similar between the Normal face condition and the Wollaston condition. This correspondence is consistent with the interpretation that the attractive influence of head rotation seen in Wollaston's effect reflects visual function that normally compensates for the repulsive effect occurring through the change in the visible part of the eye to maintain gaze constancy (Otsuka et al., 2014). One may point out that the Wollaston condition in the current study, as with Wollaston's original demonstration, involves a physically impossible configuration of the face that does not occur in real-world situations. However, our results indicate that the Wollaston effect reflects visual function that normally operates in real-world situations (corresponding to the Normal condition in the current study) to maintain gaze constancy.

Our finding that upright and inverted faces yielded similar levels of gaze constancy shows that the dual-route model applies to the perception of gaze direction in inverted faces as well as in upright faces. Thus, our results revealed little evidence that facial inversion impairs the integration of information from the eyes with information about head rotation for gaze processing. Our results are consistent with previous studies that reported an influence of head rotation on perceived gaze direction even for inverted images (Langton et al., 2004; Maruyama & Endo, 1984), and with a study that reported no effect of inversion on the discrimination of head rotation (Wilson, Wilkinson, Lin, & Castillo, 2000). The lack of an effect of inversion on integration contrasts with findings on face identity perception (e.g., Young et al., 1987). While it is generally accepted that changeable aspects of faces such as expression and gaze perception are processed by distinct mechanisms that are dissociable from those processing facial identity (e.g., Haxby, Hoffman, & Gobbini, 2000), there is evidence suggesting that some aspects of the feature integration process are shared between the processing of identity and the processing of changeable aspects of faces. For example, Calder and colleagues (Calder & Jansen, 2005; Calder, Young, Keane, & Dean, 2000) have reported a similar disruptive influence of facial inversion on the composite effect for facial expression as is found for facial identity (e.g., Young et al., 1987; Hole, 1994; Hole, George, & Dunsmore, 1999). Based on such evidence, Calder and Jansen (2005) suggested that the perceptual integration processing of facial features for both identity and expression may operate at the same level of holistic encoding where facial features are integrated into a single Gestalt representation. The lack of any inversion effect on the integration of information from the eyes with information about head rotation found in the current study suggests that the cue integration process in gaze perception does not involve such a holistic encoding process.

Although facial inversion had little effect on the integration of information from the eyes with information about head rotation, we observed a tendency for facial inversion to increase the proportion of "direct" responses. It has previously been shown that people tend to report "direct" gaze when the eyes are made less visible (Mareschal, Calder, & Clifford, 2013; Mareschal, Calder, Dadds, & Clifford, 2013; Martin & Jones, 1982; Martin & Rovira, 1981). Although the eyes were always clearly visible in the current study, our participants may have experienced greater difficulty in judging gaze direction in the inverted condition resulting in a higher proportion of "direct" responses. This result is consistent with previous reports of a broader "cone of direct gaze" associated with face inversion (Vida et al., 2013), and with impaired precision of gaze discrimination for inverted faces and eyes (Jenkins & Langton, 2003; Schwaninger, Lobmaier, & Fischer, 2005).

Our vision displays a number of well-studied constancies (Walsh & Kulikowski, 1998). Our color vision, for example, must contend with the fact that the spectral content of light reaching our eyes from an object depends not only on the surface properties of that object but also on the spectrum of the light with which it is illuminated (see Foster, 2011 for a review). Nonetheless, our visual system is able to discount the effect of illumination to a large extent, such that the perceived color of an object varies little with changes in the light source. In the context of gaze perception, cues to the deviation of the eyes are confounded by the rotation of the head. Nonetheless, our data show that even when only the eyes are visible (Eyes-only condition), subjects show a high degree of gaze constancy (approximately 0.7). This reliability is presumably achieved by using information from the projected shape of the eye to infer head rotation, perhaps coupled with a tendency to underestimate the magnitude of eye deviation (Mareschal et al., 2013).

When full cues to head rotation are available (Normal condition), gaze constancy improves to around 0.8. In the Wollaston condition, where the head is oriented but the eyes are presented in full face view, we observed over-constancy (a gaze constancy index significantly above unity) which we interpret as a result of misapplied constancy scaling. In all these conditions, our results demonstrate that upright and inverted faces yield similar levels of gaze constancy. We believe our stimulus allows a meaningful comparison of the associated constancy indices. However, it is important to acknowledge that the precise value of the gaze constancy index will likely vary with other aspects of the viewing conditions (e.g., viewing distance, image size), as is the case with indices of color constancy (Foster, 2011). Nonetheless, we anticipate that the definition of such a dimensionless index will facilitate comparison not only between future studies of gaze perception but also with studies of perceptual constancies in other domains.

Keywords: perceptual constancy, gaze perception, cue combination, face inversion, Wollaston effect

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Appendix

Derivation of Equation 2 used to infer the weighting on the direct cue of head rotation in the Normal condition

The perceived direction of gaze was modeled as a weighted average of the eye deviation and head rotation, such that two weights were constrained to sum to one:

$$G = \left(\frac{1}{1-m}\right)E + \left(\frac{m}{m-1}\right)H. \quad (1)$$

Thus, for the normal condition we can model the perceived direction of gaze, G_{NORMAL}, as:

$$G_{NORMAL} = \beta E + (1-\beta)H \quad \text{(A1)}$$

where

$$\beta = \left(\frac{1}{1-m_{NORMAL}}\right) \quad \text{(A2)}$$

and m_{NORMAL} is the slope of the regression line of the

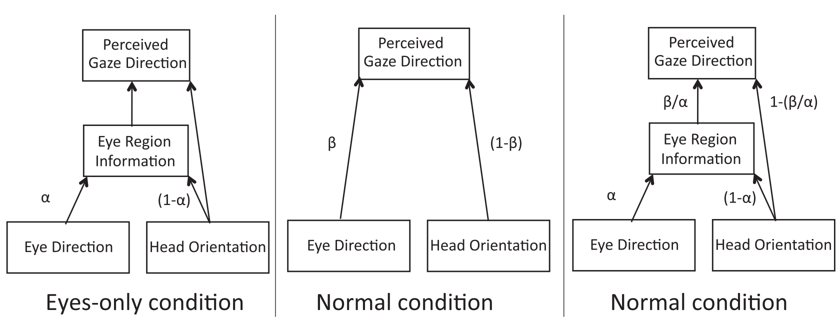

Figure A1. Illustration of the functional significance of the weights α and β in the context of the dual-route model (Otsuka et al., 2014) as applied to the Eyes-only and Normal conditions. Specifically, α represents the contribution of eye direction to eye region information in the eyes-only condition while β represents the weight attached to eye direction in the Normal condition. The weighting of head rotation as a direct cue in the Normal condition is modelled as 1–(β/α), as in Equation A6.

eye deviation corresponding to subjectively direct gaze as a function of head rotation in the Normal condition.

Similarly, for the eyes-only condition:

$$G_{EYES\text{-}ONLY} = \alpha E + (1 - \alpha)H \tag{A3}$$

where

$$\alpha = \left(\frac{1}{1 - m_{EYES\text{-}ONLY}}\right). \tag{A4}$$

In the Normal condition, the weighting, $(1 - \beta)$, attached to head rotation reflects the aggregate effect of head rotation on eye region information (indirect cue) and as an explicit cue to gaze direction in its own right (direct cue). By rearranging Equation A1 and substituting in Equation A3, we can express the perceived direction of gaze in the Normal condition, G_{NORMAL}, as a weighted average of the perceived direction of gaze in the eyes-only condition, $G_{EYES\text{-}ONLY}$, and head rotation as a direct cue.

Rearranging Equation A1:

$$G_{NORMAL} = \frac{\beta}{\alpha}\Big(aE + (1 - \alpha)H\Big) + H\left((1 - \beta) - \frac{\beta}{\alpha}(1 - \alpha)\right). \tag{A5}$$

Substituting Equation A3 into Equation A5:

$$G_{NORMAL} = \frac{\beta}{\alpha} G_{EYES\text{-}ONLY} + H\left(1 - \frac{\beta}{\alpha}\right). \tag{A6}$$

Substituting for α and β from Equations A4 and A2, respectively, into Equation A6:

$$G_{NORMAL} = \left(\frac{1 - m_{EYES\text{-}ONLY}}{1 - m_{NORMAL}}\right) G_{EYES\text{-}ONLY} + \left(\frac{m_{NORMAL} - m_{EYES\text{-}ONLY}}{m_{NORMAL} - 1}\right) H. \tag{2}$$

For the Normal condition, this estimate of the weighting on H was reported as the weighting of head rotation as a direct cue.