



# The center of attention: Metamers, sensitivity, and bias in the emergent perception of gaze



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## ABSTRACT

A person's gaze reveals much about their focus of attention and intentions. Sensitive perception of gaze is thus highly relevant for social interaction, especially when it is directed toward the viewer. Yet observers also tend to overestimate the likelihood that gaze is directed toward them. How might the visual system balance these competing goals, maximizing sensitivity for discriminating gazes that are relatively direct, while at the same time allowing many gazes to appear as if they look toward the viewer? Perceiving gaze is an emergent visual process that involves integrating information from the eyes with the rotation of the head. Here, we examined whether the visual system leverages emergent representation to balance these competing goals. We measured perceived gaze for a large range of pupil and head combinations and found that head rotation has a nonlinear influence on a person's apparent direction of looking, especially when pupil rotations are relatively direct. These perceptual distortions could serve to expand representational space and thereby enhance discriminability of gazes that are relatively direct. We also found that the emergent perception of gaze supports an abundance of direct gaze metamers—different combinations of head and pupil rotations that combine to generate the appearance of gaze directed toward the observer. Our results thus demonstrate a way in which the visual system flexibly integrates information from facial features to optimize social perception. Many gazes can be made to look toward you, yet similar gazes need not appear alike.

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## 1. Introduction

Perceiving a person's gaze direction is critical for understanding and predicting their behaviors and intentions (Allison, Puce, & McCarthy, 2000; Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & Walker, 1995; Itier & Batty, 2009). Perceiving when a person is looking directly at you is particularly important because it is a strong predictor that a social interaction may occur (Emery, 2000). Accordingly, the visual system has developed notable sensitivity for perceiving direct gaze (Cline, 1967). Direct eye contact is represented by distinct visual mechanisms (Calder, Cassel, Jenkins, & Clifford, 2008), it is detected faster than averted gaze (Senju, Kikuchi, Hasegawa, Tojo, & Osanai, 2008), and it uniquely captures visuo-spatial attention (Senju & Hasegawa, 2005). This sensitivity is in place even during childhood. For example, infants

look at faces with direct eye gaze longer than faces with indirect gaze (Farroni, Csibra, Simion, & Johnson, 2002), children are more sensitive to horizontal compared to vertical pupil displacement at the age of eight (Vida & Maurer, 2012), and infrequent exposure to direct eye contact early in life is known to disrupt typical deployment of spatial attention during communication (Senju et al., 2015).

Despite their importance, or perhaps because of it, people tend not to see relatively direct gazes exactly as they are. That is, people tend to overestimate the likelihood that others are looking towards them under conditions of perceptual uncertainty (Clifford, Mareschal, Otsuka, & Watson, 2015; Mareschal, Calder, & Clifford, 2013), but they also underestimate the likelihood that gaze is direct when information from a face is clearly visible (Anstis, Mayhew, & Morley, 1969; Otsuka, Mareschal, & Clifford, 2016). The visual system thus appears to be faced with a pair of competing challenges. First, representational space should be expanded for gazes that are relatively direct, as these are the kinds of gazes that are arguably the most important. Such a

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design would make subtle differences between gazes near the category boundary of left/right appear more distinct and thus easier to discriminate. Second, the visual system should accommodate a prior for seeing direct gaze often and allow many gazes to appear as if they look toward the viewer—a direct gaze bias. This bias would ensure that when gaze is direct (or nearly direct), it is seen as such. In other words, people should be good at perceiving relatively direct gazes, yet at the same time misperceive many gazes as direct. Here, we examine how emergent gaze representation may distort the appearance of a person's direction of looking, and thus allow the visual system to balance these seemingly contradictory goals.

Although altering a feature's appearance to improve perception may seem paradoxical, this process can actually be beneficial when that feature has a value near a category boundary. As long as the distortion is systematic, it can decrease the opportunity for random sensory noise to cause across-category perceptual errors (Kourtzi, 2010). Indeed, the visual system often sharpens perception around category boundaries (Ball & Sekuler, 1980, 1982; Bornstein & Korda, 1984; Etcoff & Magee, 1992; Ferrera & Wilson, 1990; Harnad, 1987; Heeley & Buchanan-Smith, 1992; Liberman, Harris, Hoffman, & Griffith, 1957; Matthews & Welch, 1997), and this sensitivity in turn produces perceptual distortions. For example, discrimination of biological motion is best for direct trajectories, and this sensitivity repels the perceived walking direction of a person away from the leftward/rightward category boundary (Sweeny, Haroz, & Whitney, 2012). Similar distortions enhance the perception of local motion trajectories (Rauber & Treue, 1998), facial identity (McKone, Martini, & Nakayama, 2001), and multi-modal perception of gender (Smith, Grabowecky, & Suzuki, 2007). We predicted that similar kinds of mechanisms would influence the perception of gaze, but not just the local perception of pupil rotation. Rather, we expected perceptual distortions to emerge at the level of emergent gaze, when a person's direction of looking is determined not just by the rotation of the pupils within the aperture of the eye, but the face and head as well.

Gaze is perceived by integrating local information from the eyes with the rotation of the head. This interaction produces a striking percept—the Wollaston effect—where a person's perceived gaze direction is pulled by the rotation of the head (Cline, 1967; Kluttz, Mayes, West, & Kerby, 2009; Langton, Honeyman, & Tessler, 2004; Murayama & Endo, 1984; Otsuka, Mareschal, Calder, & Clifford, 2014; Wollaston, 1824). The perceived gaze that results from this integration is carried neither by the pupils nor by the head alone, and thus has a unique quality. We refer to this distinct percept as emergent gaze. Very recently, an investigation conducted in parallel with our own showed that, at least in some circumstances, this integration is the result of a linear combination of information from the head and eyes (Otsuka et al., 2016). Here, using a design with some notable differences, we tested the hypothesis that the visual system leverages this integrative process to simultaneously enhance representation of relatively direct gazes, and at the same time, allow many kinds of gazes to appear to be direct. First, we predicted that head rotations would distort perceived gaze most strongly when pupil rotations are relatively direct, thereby expanding representational space for discriminating the most important kinds of gazes. And since sensitivity for discriminating head rotation peaks near the left-vs.-right category boundary (Wilson, Wilkinson, Li-Ming, & Castillo, 2000), we predicted that head rotations near this boundary would exert a particularly strong pull on perceived gaze. Second, we predicted that the increased range of gaze percepts that result from these emergent distortions should also produce an abundance of direct gaze metamers—different combinations of head and pupil rotations

that combine to generate the appearance of gaze directed at the observer.

## 2. Experiment 1

### 2.1. Materials and method

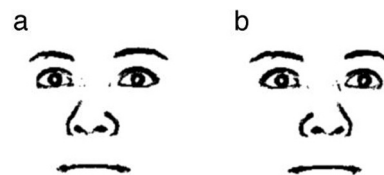
#### 2.1.1. Observers

Nine observers (eight naïve) provided informed consent. All had normal or corrected-to-normal visual acuity and were tested individually in a dimly lit room. All work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

#### 2.1.2. Stimuli

We manipulated gaze at the level of an emergent feature, in which a person's apparent direction of looking is determined by integrating local pupil information with the rotation of the head (Wollaston, 1824). Fig. 1 illustrates one example of this phenomenon. Here, the rotations of the irises/pupils within the apertures of each pair of eyes are identical, yet they appear to have leftward or rightward gazes by virtue of being superimposed onto heads with subtle leftward or rightward rotations, respectively. We note that internal features, like the nose, are sufficient for discriminating head rotation (Wilson et al., 2000) and produce strong attractive effects on perceived gaze (Langton et al., 2004). We also note that this attractive effect from the head is distinct from a separate effect that emerges from the appearance of the eyes (Anstis et al., 1969; Gibson & Pick, 1963; Mareschal et al., 2013). When a head turns, the size and shape of one eye's aperture appears to change more quickly than the other's, at least from the perspective of the viewer, and this change influences the perception of the iris and pupil within that aperture. Unlike a head rotation in the same direction, this change in local information from the eyes actually repels the perceived direction of gaze. These attractive and repulsive effects from the head and eyes are likely to be related and potentially complementary (Otsuka et al., 2014, 2016), and the extent to which one dominates the other likely depends on the relative visibility of information from the head or eyes (Gamer & Hecht, 2007). For simplicity we focus here on the attractive effect from the rotation of the head. In particular, we use stimuli reminiscent of those from Wollaston's original investigation of gaze (Wollaston, 1824) and several others thereafter, where the shape and size of the eye apertures never change despite rotation of the head.

We aimed to examine the perception of gaze across a wide range of head and pupil rotations. We thus created a set of 144 computer-generated faces by independently manipulating head rotation and pupil rotation (Face Gen Modeller, Version 3.5.5, Singular Inversions, 2009). First, we created heads with nine degrees of horizontal rotation ( $-8^\circ$ ,  $-6^\circ$ ,  $-4^\circ$ ,  $-2^\circ$ ,  $0^\circ$ ,  $+2^\circ$ ,  $+4^\circ$ ,  $+6^\circ$ , and  $+8^\circ$ ; turning from the observer's left to right, respectively). Next,



**Fig. 1.** Eyes with identical pupil rotations appear to have unique gaze directions when coupled with (a) leftward or (b) rightward head rotations. Note that, in both images, the shapes of the scleras (the white regions of the eyes) and the positions of the pupils and irises within the scleras are identical. The shading information nearby the eyes, as well as the eyebrows, noses, and mouths was allowed to vary.

we used a head with a straightforward rotation ( $0^\circ$ ) to generate 16 pupil rotations around a vertical axis ( $-75\%$ ,  $-65\%$ ,  $-55\%$ ,  $-45\%$ ,  $-35\%$ ,  $-25\%$ ,  $-15\%$ ,  $-5\%$ ,  $+5\%$ ,  $+15\%$ ,  $+25\%$ ,  $+35\%$ ,  $+45\%$ ,  $+55\%$ ,  $+65\%$ , and  $+75\%$ ). Note that unlike with the head rotations, these values reflect the percentage, and not the degrees, of a given pupil or iris' simulated rotation within the eye opening of a three-dimensional head. A value of zero indicates a direct gaze. A value of  $+75$  indicates that, relative to its position when gaze is direct, the outside edge of the iris has been rotated 75% of the distance to the edge of the eye aperture.<sup>1</sup> We then used Photoshop (Adobe Photoshop CS5 Version 12.0) to extract each pair of these rotated pupils (and the iris and sclera, up to the surrounding eye contours, but not including any information from the skin), which we then superimposed onto each rotated head. In doing so, we were able to create faces in which the head rotation varied, but the rotation, size, and shape of the eye apertures did not. Combining nine head rotations with sixteen pupil rotations produced 144 test faces.

We schematized the faces using a three-step process in Photoshop. First, we eliminated the contour of the head and chin. Next, we applied a high-pass filter with a four-pixel radius. Then, we applied a threshold to the image (at a level of 120 in the thresholding tool) rendering pixels either black or white. Last, we applied a Gaussian blur with a 0.4 pixel radius. This procedure eliminated most shading information and it equated all faces in terms of low-level visual information (reproduced from Sweeny & Whitney, 2014). Most importantly, the shapes and sizes of the eye apertures never changed even though some shading information nearby the eyes was preserved, as in Wollaston's original study of emergent gaze (Wollaston, 1824). Each face subtended  $1.01^\circ \times 0.84^\circ$  of visual angle.

### 2.1.3. Procedure

Every observer viewed each of the 144 head-pupil combinations on a test face presented on the top half of the screen (the center of the face was  $1.26^\circ$  above fixation). Observers were told to imagine that the test face was looking out toward a point in space and to adjust the pupil rotation on a separate response face with a straightforward head ( $0^\circ$  horizontal rotation) so that its direction of gaze appeared to match that of the test face. The response face was presented at the same time as the test face, and on the bottom half of the screen ( $1.26^\circ$  below fixation). Only the pupil positions of the response face could be rotated in 10% increments between  $-95\%$  and  $+95\%$  (we created these additional pupil rotations for the response face using the same approach described in the Stimuli section). The starting pupil position on the response face was randomly selected on each trial from a uniform distribution between  $-95\%$  and  $+95\%$ . The test face and response face remained on the screen until the observer pressed the spacebar. Observers were encouraged to look at both of the faces, although they were instructed to fixate only the bridge of each face's nose. They had an unlimited amount of time to respond and were encouraged to be as careful as possible. We recorded the pupil rotation on the response face (e.g.,  $-5\%$ , looking slightly toward the observer's left)

<sup>1</sup> We anticipate that some readers may wish to translate our effects to more familiar units of degrees of rotation. Although FaceGen (the software we used to create our stimuli) does not provide this information, we were able to make a reasonable estimate by recreating our stimuli as seen from a "worm's eye" view (i.e., looking up toward the chin) in which the curvature of the eye is visible. For any given eye rotation, one simply needs to extend a line perpendicular to the orientation of the iris and pupil along the curvature of the eye, away from the face. Calculating rotation in terms of degrees is then a matter of determining the angle between this line of gaze and the line that would emerge from a direct gaze (note that the gazes in FaceGen do not converge on a horopter). We determined that one unit of rotation in FaceGen equated to roughly  $0.28^\circ$  of pupil rotation. According to this conversion, the 10% steps in our response face reflected fine adjustments of about  $2.8^\circ$ , and the range of gazes tested was about  $\pm 26^\circ$ . Although we are confident in this conversion, it is still an estimate, thus we present our stimuli, analyses, and results in terms of % rotation.

as the perceived gaze direction for each of the 144 head-pupil combinations (note that much of the description of this methodology is reproduced from Sweeny & Whitney, 2014). Each test face was shown once for a total of 144 trials. All stimuli were presented on a 61-cm LCD monitor at a viewing distance of 102 cm.

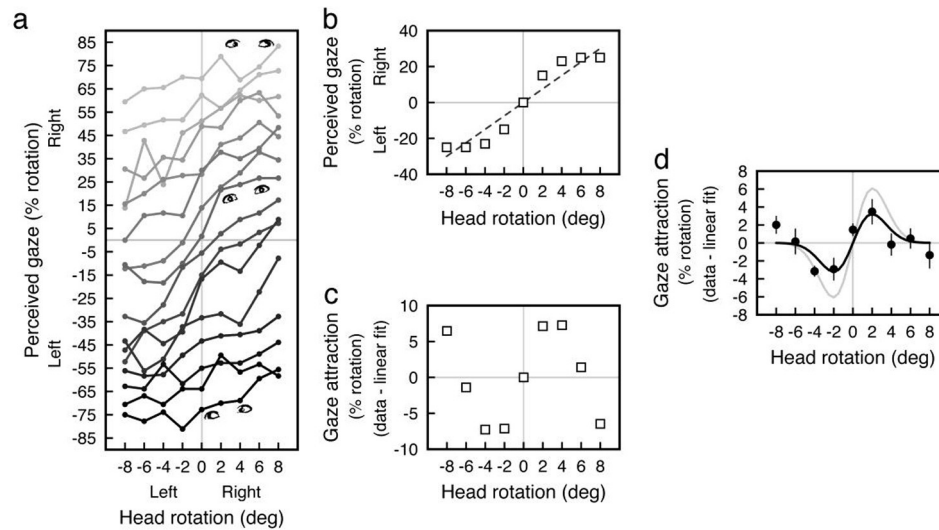
## 3. Results

### 3.1. Replicating the Wollaston effect

Our first objective was to evaluate whether head rotations attracted perceived gaze, as in a previous investigation with these same stimuli (Sweeny & Whitney, 2014). We thus conducted a repeated-measures analysis of variance (nine head rotations and sixteen pupil rotations) on reports of perceived gaze. A main effect of head rotation confirmed that perceived gaze was indeed pulled in the direction of the head's rotation,  $F(8,63) = 51.88$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.87$ ; (note the positive slopes in Fig. 2a). When this effect of head rotation was collapsed across the different pupil rotations, a linear fit explained the data well, accounted for 97.23% of the variance. A main effect of pupil rotation confirmed that observers were also clearly sensitive to differences in the positions of the pupils within the eye apertures, irrespective of head rotation,  $F(15,119) = 375.59$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.98$  (note the vertical spacing between each line in Fig. 2a). More interestingly, the interaction between head rotation and pupil rotation was significant,  $F(120,959) = 2.43$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.23$ . This suggests that (1) some pupil rotations may have been more susceptible to the influence of head rotation than others, and/or (2) some head rotations may have influenced perceived gaze more than others. Next, we discuss the results of follow-up analyses designed to test these predictions. We work through these predictions in reverse order; first examining whether head rotations near the category boundary had the strongest pull on perceived gaze. This allowed us to determine whether non-linear fits would provide the most appropriate means for extracting the slopes of the lines in Fig. 2a (as we predicted), before then using these slopes as an index of emergent gaze strength across different pupil rotations.

### 3.2. Do head rotations near the category boundary exert a stronger pull on perceived gaze?

We predicted that head rotations near the category boundary (e.g.,  $+2^\circ$ ) would attract perceived gaze more strongly than head rotations further from the category boundary (e.g.,  $+8^\circ$ ). Put another way, even though a linear fit provided an excellent characterization of the effect of head rotation on perceived gaze, we expected a specific non-linear pattern to emerge in the residuals to this fit. To test this hypothesis, we started by first obtaining a linear fit to each observer's reports of perceived gaze across the nine head rotations, separately for each of the 16 pupil rotations (e.g., one fit for data from trials with  $-5\%$  pupils, another fit for data from trials  $+5\%$  pupils, etc.). Then, for each data point, we calculated the difference between each observer's reported gaze and the gaze predicted by each linear fit (see hypothetical example in Fig. 2b). Hypothetically, if each of the nine head rotations were to exert an equivalent pull on perceived gaze, then each data point should fall along the linear fit, each producing a difference score of zero. However, if head rotations near the category boundary exert a relatively strong pull on perceived gaze, we should obtain a unique s-shaped pattern of difference scores (Fig. 2c). Specifically, heads rotated slightly to the right should pull gaze more than predicted by the linear fit, producing positive difference scores. The converse should be true for heads rotated slightly to the left. Across the nine head rotations, this pattern of increased attraction should



**Fig. 2.** Effects of integrating head and pupil rotation on gaze perception in Experiment 1. (a) Head rotation (shown along the x-axis) pulled the perceived gaze direction (y-axis) of eyes with 16 different pupil rotations (each corresponding to one line). Positive slopes for each line depict the change in perceived gaze direction when each unique pair of pupil rotations was paired with nine different head rotations. If head rotation had no influence on perceived gaze, all lines would be flat. Data are from all nine observers. Based on our conversion of pupil rotation to degrees (see footnote 1), the 10% increments along the y-axis reflect pupil rotations of approximately  $2.8^\circ$ . (b) A linear fit superimposed over hypothetical data that would emerge if head rotations near the category boundary (e.g.,  $-2^\circ$ ) pulled perceived gaze more strongly than head rotations further from the category boundary (e.g.,  $-6^\circ$ ). (c) The difference between the hypothetical data and the linear fit in panel B. Positive values indicate the amount of gaze attraction beyond that predicted by the linear fit in panel B. These hypothetical difference scores follow the first derivative of a Gaussian function (i.e., an s-shape). (d) Actual data from all nine observers (collapsed across all pupil rotations) were well fit by the derivative of a Gaussian function, demonstrating that head rotations near the category boundary attracted perceived gaze more strongly than head rotations further from the category boundary. The black line depicts a fit to data averaged across all pupil rotations and the gray line depicts a fit to data averaged across relatively direct pupil rotations. Error bars in panels D represent  $\pm 1$  SEM, adjusted for within-observer comparisons.

be strongest near the category boundary and taper off with greater positive and negative values of head rotation, roughly following the first derivative of a Gaussian function (Fig. 2c; e.g., Sweeny et al., 2012).

Averaged across all nine observers, the magnitude of these difference scores was well fit by the derivative of a Gaussian function ( $R^2 = 0.64$ ,  $p < 0.001$ , see the black line in Fig. 2d). The s-shape of the function is consistent with a flip in the direction of attraction around the  $0^\circ$  head rotation (directly toward the observer), and the full-amplitude of the function (6.42%) indicates the maximum amount of attraction across the different head rotations beyond that predicted by a linear fit. The quality of this fit indicates that the non-linear pattern accounted for 63.89% of the remaining variance after the linear effect of head rotation, or 1.77% of the total variance. Interestingly, this non-linear effect was especially strong when heads were combined with relatively direct pupils ( $-25\%$  through  $+25\%$ , representing roughly the middle of the response range,  $R^2 = 0.72$ ,  $p < 0.001$ ), with a full-amplitude of 12.14% (see the gray s-curve with the large amplitude in Fig. 2d). For relatively direct pupils, this non-linearity accounted for 3.49% of the total variance in gaze perception.

Although this non-linear effect may seem subtle, there are several reasons why it is impactful and valuable to consider. First, at its strongest (a full amplitude of 12.1%, or  $\sim 3.4^\circ$ ), it created distortions of gaze greater than the smallest differences observers were just able to notice with our stimuli (JND = 9.3% or  $\sim 2.6^\circ$ ). We derived this group-level JND from the distributions of response errors from all pupil rotations from all observers. It thus includes cross-observer error and therefore represents a conservative estimate of gaze sensitivity relative to JNDs from previous investigations (e.g., a JND of  $0.7^\circ$  in Cline, 1967). This non-linear interaction was thus strong enough to cause two otherwise identical gaze directions to appear noticeably different. Second, this non-linear effect was reliable, with good fits indicating that it is important to consider in addition to linear processes in order to fully

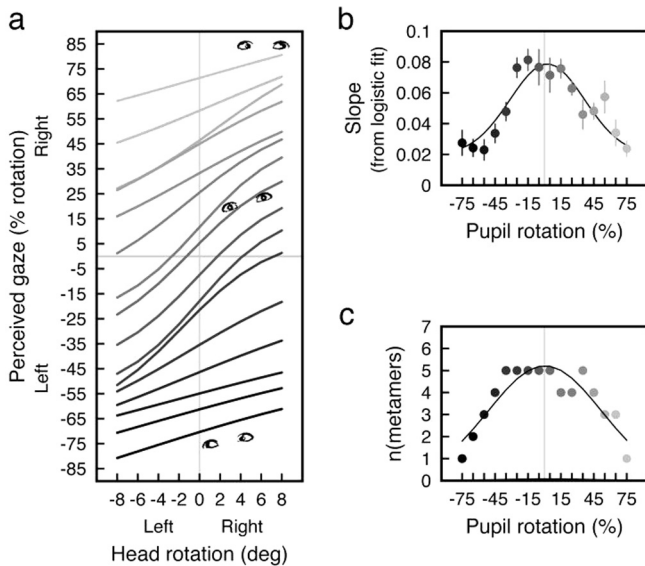
understand gaze perception, at least in some circumstances (Otsuka et al., 2016). Third, accounting for this effect allowed us to move on to our main objective—determining if the process of emergent representation produces an abundance of direct gaze metamers.

### 3.3. Are pupil rotations near the category boundary more strongly influenced by head rotation?

Our next objective was to evaluate whether head rotations influenced the perception of relatively direct pupil rotations (e.g.,  $-5\%$ ) more strongly than pupil rotations far from the category boundary (e.g.,  $-65\%$ ). We started by first obtaining a logistic fit for each observer's reports of perceived gaze across the nine head rotations, separately for each of the 16 pupil rotations (Fig. 3a).<sup>2</sup> This approach, as opposed to obtaining linear fits, is justified by the non-linear pattern of distortions described in the previous section (see Section 3.2). The slope of each fit indicated the extent to which head rotations influenced perceived gaze, with greater slopes indicating stronger attraction.

Averaged across the nine observers, the distribution of slopes across the 16 pupil rotations was well fit by a Gaussian function ( $R^2 = 0.87$ ,  $p < 0.001$ , Fig. 3b). In other words, slopes were steeper

<sup>2</sup> It was not possible to fit our data using a logistic function with a traditional ceiling value of 1.0. Instead, we used a ceiling value of 220 to accommodate the large range of response values ( $-95\%$  to  $+95\%$ ) in our experiment. We obtained this value in the following way. First, we normalized each series of reported gaze values around the actual value of pupil rotation. For example, when the target face's pupil rotation was  $+5\%$ , an observer might have provided nine perceived gaze values (e.g.,  $-20$ ,  $-20$ ,  $-18$ ,  $-10$ ,  $+5$ ,  $+20$ ,  $+28$ ,  $+30$ , and  $+30$ ), one associated with each value of head rotation. We then normalized these data against the actual pupil rotation of  $+5\%$ , producing a new series of data ( $-25$ ,  $-25$ ,  $-23$ ,  $-15$ ,  $0$ ,  $+15$ ,  $+23$ ,  $+25$ , and  $+25$ ). Doing so for each observer and for each value of pupil rotation revealed the full spectrum of response "errors" ( $-150\%$  to  $+70\%$ , range of 220%) across our entire data set. We then obtained our logistic fits on each normalized series of data, always using this same range in our calculations.



**Fig. 3.** Effects of integrating head and pupil rotation on gaze perception in Experiment 1. (a) Logistic fits for averaged data from Experiment 1 depicting the influence of head rotation (shown along the x-axis) on perceived gaze direction (y-axis) for each set of eyes with 16 different pupil rotations (each corresponding to one fit). Note that raw data for these fits are depicted in Fig. 2a. (b) Slopes of each line from panel a, calculated separately for each observer and then averaged. Head rotations had the strongest attractive influence on the perceived gaze of pupil rotations near the category boundary. Error bars in this panel represent  $\pm 1$  SEM, adjusted for within-observer comparisons. (c) The number of pupil and head combinations that were able to produce each of the particular directions of perceived gaze responses in Experiment 1. Metamers—the same percept arising from different visual patterns—were more common for relatively direct gaze directions.

for fits to relatively direct pupils, indicating that head rotations influenced these gazes most strongly. This Gaussian fit characterized the data better than a linear function (linear  $R^2 = 0.02$ , *n.s.*). We note that we obtained a very similar Gaussian-shaped distribution when we fit each observer's data with linear functions and plotted the average of the resulting slopes ( $R^2 = 0.82$ ,  $p < 0.001$ ). The peak of the Gaussian fit (2.61%, 95% CIs:  $-4.48$  and  $9.65$ ) was centered close to zero. This pattern shows that gaze attraction was not uniform across the range of pupil rotations, but was maximal for rotations near the category boundary.

### 3.4. Direct-gaze metamers

The positive slopes in Fig. 3a illustrate an intriguing aspect of emergent gaze perception; physically different combinations of heads and pupils can appear to have the same direction of gaze. The stronger the influence of head rotation on perceived gaze, the more likely these gaze metamers are to occur. It thus follows that in our experiment, gaze metamers should have been more prevalent when pupil rotations were relatively direct. Evaluating this possibility was our primary objective. We thus counted the number of pupil and head combinations that were able to produce each of the particular directions of perceived gaze in our experiment (Fig. 3c). For example, a horizontal line drawn across the perceived gaze value of +5% in Fig. 3a would intersect five lines, with each intersection indicating a unique combination of head and pupil rotation that was perceived as looking +5% to the observer's right. We counted the number of times each perceived gaze response option from Experiment 1 ( $-95\%$  to  $+95\%$ , in 10% increments) intersected with the logistic fits to the perceived gaze data averaged across all nine observers. Clearly, gaze metamers were more prevalent for relatively direct gazes, illustrated by the

Gaussian-shaped distribution in Fig. 3c ( $R^2 = 0.81$ ,  $p < 0.0001$ ). This fit characterized the pattern of data better than a linear function (linear  $R^2 = 0.0006$ , *n.s.*).

Overall, the results of this experiment provide converging evidence that the visual system strikes a balance between seeing relatively direct gazes often, and discriminating these gazes with increased sensitivity. This sensitivity occurred not in terms of seeing gaze exactly as it was. Rather, at least when the head or eyes were relatively direct, small changes in a face resulted in large changes in perceived gaze. This should have allowed observers to notice and therefore discriminate subtle changes in actual gaze even though what they perceived may not have been entirely accurate.

## 4. Experiment 2

In Experiment 1, observers adjusted the pupils of a response face that included other internal facial features. When comparing the response face's gaze to that of the test face, observers were thus comparing two emergent, integrated percepts of gaze. It is unclear what effect this response setup might have had on our results. We conducted Experiment 2 to evaluate whether our results would replicate with a simpler response setup. Experiment 2 was identical to Experiment 1 except that observers adjusted the horizontal rotation of a pair of pupils that were not surrounded by internal facial features.

### 4.1. Materials and method

#### 2.1.4. Observers

The same nine observers from Experiment 1 gave informed consent.

#### 2.1.5. Stimuli and procedure

The stimuli and procedure were identical to those in Experiment 1, except that the response face only featured a pair of pupils and surrounding eye contours, but did not include other internal facial features (nose, eyebrows, or mouth).

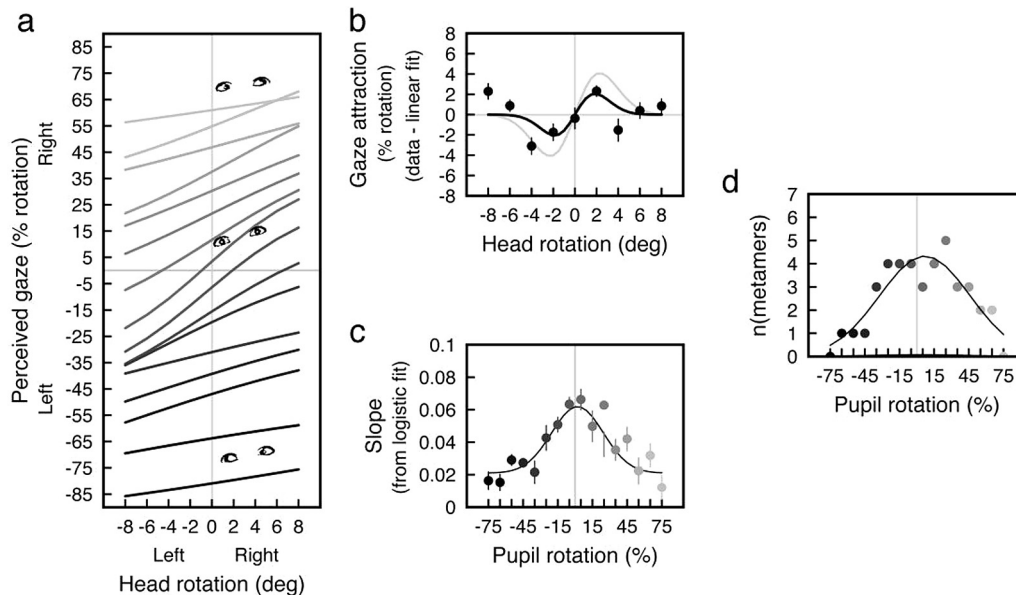
## 5. Results

### 5.1. Replicating the Wollaston effect

As in Experiment 1, a repeated-measures analysis of variance (nine head rotations and sixteen pupil rotations) confirmed that perceived gaze was pulled in the direction of the head's rotation,  $F(8,63) = 29.06$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.79$  (Fig. 4a). When this effect of head rotation was collapsed across the different pupil rotations, a linear fit explained the data well, accounting for 96.11% of the variance. A main effect of pupil rotation also confirmed that observers were sensitive to differences in the positions of the pupils within the eye apertures, irrespective of head rotation,  $F(15,120) = 443.8$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.98$ . As in Experiment 1, the interaction between head rotation and pupil rotation was significant,  $F(120,960) = 2.36$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.23$ .

### 5.2. Do head rotations near the category boundary exert a stronger pull on perceived gaze?

Averaged across all nine observers, non-linear gaze distortions beyond those predicted by the linear fits tended to be well fit by the derivative of a Gaussian function ( $R^2 = 0.34$ ,  $p = 0.07$ , Fig. 4b). The full-amplitude of the function (4.1%) was lower than that for the data from Experiment 1, suggesting a reduction in the amount of gaze attraction in Experiment 2 (we confirm this with a mixed-



**Fig. 4.** Effects of integrating head and pupil rotation on gaze perception in Experiment 2. (a) Logistic fits to averaged data depicting the influence of head rotation (shown along the x-axis) on perceived gaze direction (y-axis) for each set of eyes with 16 different pupil rotations (each corresponding to one fit). Raw data are not shown for this experiment. (b) Difference scores between the actual data from all 9 observers and a linear fit to these data followed the first derivative of a Gaussian function (i.e., an s-shape), demonstrating that head rotations near the category boundary attracted perceived gaze more strongly than head rotations further from the category boundary. The black line depicts a fit to data averaged across all pupil rotations and the gray line depicts a fit to data averaged only across relatively direct pupil rotations. (c) Slopes of each line from panel A, calculated separately for each observer and then averaged. Head rotations had the strongest influence on the perceived gaze of pupil rotations near the category boundary. (d) The number of pupil and head combinations that were able to produce each of the particular directions of perceived gaze in Experiment 2. Metamers were more common for relatively direct gaze directions. Error bars in panels B and C represent  $\pm 1$  SEM, adjusted for within-observer comparisons.

ANOVA, described below). This non-linear pattern accounted for 1.33% of the total variance on top of the linear fit. Although this value may seem small, as in Experiment 1, the strength of this non-linear effect was stronger when heads were combined with relatively direct pupils ( $-25\%$  through  $+25\%$ , roughly the middle of the response range,  $R^2 = 0.54$ ,  $p < 0.05$ ), with a full-amplitude of 8.1% (see the gray s-curve with the large amplitude in Fig. 4b). This non-linearity accounted for 2.9% of the total variance in gaze perception for these relatively direct gazes. Accounting for this non-linear effect allowed us to move on to our main objective—determining if the process of emergent representation produces an abundance of direct gaze metamers.

### 5.3. Are pupil rotations near the category boundary more strongly influenced by head rotation?

Averaged across the nine observers, the distribution of slopes across the 16 pupil rotations was well fit by a Gaussian function ( $R^2 = 0.83$ ,  $p < 0.001$ , Fig. 4c). This Gaussian fit characterized the data better than a linear function (linear  $R^2 = 0.015$ , *n.s.*). As in Experiment 1, the peak of the fit was shifted slightly to the right (2.07%, 95% CIs:  $-4.49$  and  $8.51$ ), but still close to zero.

### 5.4. Direct-gaze metamers

As in Experiment 1, we counted the number of pupil and head combinations that were able to produce each of the particular directions of perceived gaze response options in our experiment. We counted the number of times each perceived gaze option ( $-95\%$  to  $+95\%$ , in 10% increments) intersected with the logistic fits to the perceived gaze data averaged across all nine observers (see Fig. 4a). Once again, gaze metamers were more prevalent for relatively direct gazes, illustrated by the Gaussian-shaped distribution in Fig. 4d ( $R^2 = 0.82$ ,  $p < 0.001$ ). This fit characterized the pattern of data better than a linear function (linear  $R^2 = 0.04$ , *n.s.*).

### 5.5. Do the results of Experiment 2 differ from the results of Experiment 1?

We compared the results of Experiment 2 with those from Experiment 1 in a mixed ANOVA. The main effect of Experiment was not significant,  $F(1,15) = 0.47$ , *n.s.* However, the interaction between Experiment and Head Rotation was significant,  $F(8, 127) = 2.64$ ,  $p = 0.013$ ,  $\eta_p^2 = 0.14$ , as were the interaction between Experiment and Pupil Rotation,  $F(15,239) = 2.71$ ,  $p = 0.0007$ ,  $\eta_p^2 = 0.15$ , and the interaction between Head Rotation and Pupil Rotation,  $F(120, 1919) = 3.79$ ,  $p < 0.0001$ ,  $\eta_p^2 = 0.19$ . The three-way interaction between Experiment, Head Rotation, and Pupil Rotation was not significant,  $F(120,1919) = 1.01$ , *n.s.* In summary, these results confirm that the same pattern of results emerged in Experiment 2, albeit at a lesser magnitude. Overall, Experiment 2 provides a replication of Experiment 1, and strengthens our evidence that the visual system leverages the process of emergent representation to strike a balance between discriminating relatively direct gazes and seeing them often.

## 6. Discussion

Of the many social cues people encounter, gaze is easily among the most important (Allison et al., 2000; Baron-Cohen et al., 1995; Itier & Batty, 2009). Determining when another person is looking at you is particularly crucial. It thus makes sense that people appear to be both sensitive for discriminating relatively direct gazes and biased to report seeing gaze as direct. And yet these facts seem contradictory, at least if gaze were determined by one visual feature alone. Here, we demonstrated that the visual system leverages the process of emergent gaze representation—combining information from the pupils with the face and head (Cline, 1967; Klutetz et al., 2009; Langton et al., 2004; Murayama & Endo, 1984; Otsuka et al., 2014; Wollaston, 1824)—to balance these competing demands of sensitivity and bias. We found that when eye gaze is

relatively direct, the visual system is especially likely to utilize information from head rotation to inform judgments of where a person is looking. This is consistent with the idea that gaze representation is flexible, adding information from the head when it is available or useful (Mareschal et al., 2013; Perrett, Hietanen, Oram, & Benson, 1992). Previous work has shown that people are particularly good at discriminating direct head rotations (Wilson et al., 2000). Accordingly, we also showed that the visual system gives extra weight to head rotations nearby this category boundary during the process of emergent gaze perception. Finally, we showed that by maximizing sensitivity for discriminating direct gaze, the visual system also produces an abundance of emergent direct-gaze metamers—unique combinations of head and pupil rotations that appear to look toward the viewer.

Some of our findings differ from those of a similar investigation in which head and eye rotations were integrated linearly, and with less strength, at least when faces were relatively large ( $24^\circ \times 14^\circ$ ) and seen briefly (500-ms) (Otsuka et al., 2016). The faces in our investigation were much smaller by comparison ( $1.01^\circ \times 0.84^\circ$ ) and were available for unlimited inspection. These kinds of differences could reasonably be expected to influence the relative weighting of head and eyes in the computation of gaze, particularly if they impact the visibility or salience of these features (Florey, Clifford, Dakin, & Mareschal, 2016; Florey, Dakin, Clifford, & Mareschal, 2015; Gamer & Hecht, 2007). For example, information from the head might be weighted more heavily when a face makes a small image on the viewer's retina, as when seen from a great distance. Indeed, head and pupil rotations seem to have contributed more equally to the perception of gaze in our investigation than in a comparable condition in Otsuka et al., 2016. We thus speculate that the non-linear interactions unique to our results may be more readily apparent when these cues make more balanced contributions to perception of emergent gaze. Additionally, some of these non-linear effects, especially the most subtle ones, may be more readily observed with prolonged and detailed inspection of a face, as in the current investigation. Future work will be necessary to directly test these ideas. In the mean time, we note that the differences between our findings illustrate that emergent gaze representation may be more flexible than previously thought.

Our results add to growing evidence that human vision has evolved with an emphasis on making discriminations around categorical boundaries (Bornstein & Korda, 1984; Etcoff & Magee, 1992; Harnad, 1987; Liberman et al., 1957). Many other investigations have demonstrated that increased sensitivity around category boundaries leads to repulsive perceptual distortions (McKone et al., 2001; Rauber & Treue, 1998). For example, we previously showed that when a person's direction of walking is slightly to the right of straight-ahead (e.g.,  $+9^\circ$ ), it is nevertheless perceived as deviated even further from the category boundary (e.g.,  $+15^\circ$ ) (Sweeny et al., 2012). The current results are similar in that perception was most likely to be distorted when eye gaze was relatively direct, and this enhancement occurred most strongly with head rotations near the category boundary. These distortions appear to expand the representational space of gaze around the categorical boundary of direct-vs-indirect, and should thus make relatively direct gazes appear more distinct and easier to discriminate. Nevertheless, our findings deviate from previous work in an important way. Perceived gaze direction was not always repelled from the category boundary. In fact, many of the perceptual distortions we observed tended to make gazes appear more direct.

Our findings are predicated on the integration of face parts, and are thus likely to be rooted in high-level visual representation. Specifically, populations of cells in the macaque superior temporal sulcus (STS) respond to combinations of head and eye rotations (De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Oram & Perrett, 1992;

Perrett et al., 1985), and cells in the macaque middle face patch respond to multiple face parts when seen individually (e.g., the outline of a head or the eyes), as well as combinations of face parts (e.g., the head and the eyes). Homologous neuronal populations have also been found in humans (Calder et al., 2007; Fang, Murray, & He, 2007; Hoffman & Haxby, 2000; Pelphrey, Morris, & McCarthy, 2005; Puce, Allison, Bentin, Gore, & McCarthy, 1998), and anterior STS appears to be the locus for the integration of this information (Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011). Our results add to this work by demonstrating the flexibility with which the visual system is able to integrate information from a person's head and eyes when gaze is direct, and thus most socially relevant (Emery, 2000). By mapping out the circumstances in which emergent gaze operates most strongly, our findings lay the groundwork for future work to reveal supporting algorithms and neural mechanisms.

Gaze perception has been described as the core of social cognition (Itier & Batty, 2009). Accordingly, we have shown that the visual system flexibly utilizes information from the head and eyes to optimize the perception of gaze when it is direct, and thus of peak social relevance. More generally, our findings underscore the notion that vision has evolved not for the purpose of representing the world exactly as it is, but instead for guiding behavior and social interaction.

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