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Emergent Perception of Gaze Direction Across Time

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To determine where another person is looking, the visual system engages a process of emergent integration, pooling information across space from both the head and eyes. Gaze is dynamic, however, and in order to achieve a temporally stabilized metric of a person's direction of attention, this integrative process might also occur across time. Here, we tested and confirmed this prediction. Even when seen separately and in succession, the rotation of a head attracted the perceived gaze of a pair of eyes. This integration depended on temporal continuity—attraction decayed with longer delays between the face parts and prolonged viewing of the head reduced integration. Nevertheless, gaze integration persisted across delays of 2 s and even occurred against a backdrop of changing emotional expression. Gaze is a complex feature that orchestrates social interactions over time. Our results demonstrate that the representation and perception of emergent gaze is dynamic as well.

Public Significance Statement

This investigation provides new insights into how the human visual system builds cohesive representations of faces not just across space, but also across time. We showed that multiple facial features relevant to the perception of gaze can be integrated into a single metric of a person's direction of attention even when they are seen sequentially. These findings demonstrate the visual system's surprising flexibility for maintaining perceptual stability of complex and dynamic cues integral for nonverbal communication and social interaction.

Keywords: gaze perception, face perception, visual memory, object continuity, facial features

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Faces are a rich source of social information. Even when seen for just a moment, a person's face can reveal their identity (Bruce & Young, 1986), emotion (Haxby, Hoffman, & Gobbini, 2000), and direction of attention (Driver et al., 1999). This communicative power emerges not just because faces have many features, but also because these features convey information relatively independently (Carlin, Calder, Kriegeskorte, Nili, and Rowe, 2011; Hoffman & Haxby, 2000). Thus, when combined, facial features offer an exceptionally vast source of unique displays. Accordingly, the human visual system has evolved particular sensitivity for representing faces at the emergent level, integrating cues from spatially distinct features so that, at any moment, a face may be perceived as a unified whole (Farah, Wilson, Drain, & Tanaka, 1998; Suzuki & Cavanagh, 1995) carrying distinct information not present in any feature alone (Cline, 1967; Kluttz, Mayes, West, & Kerby, 2009; Langton, Honeyman, & Tessler, 2004; Maruyama & Endo, 1984; Otsuka, Mareschal, Calder, & Clifford, 2014; Wollaston, 1824). Yet faces are often experienced across time. In this case, social cues like a person's gaze, for example, must be seen and understood *across* multiple moments. If emergent representation is central to the process of face perception (e.g., Suzuki & Cavanagh, 1995), it should be robust to this challenge, integrating and uniting cues from different facial features into a continuous and emergent representation across time. Testing this prediction was the main goal of the current investigation.

Ours is certainly not the first investigation to point out that face perception is a temporally extended event. For example, even when seen at the same time, different parts of a face may be sequentially fixated or attended depending on the social context (Buchan, Paré, & Munhall, 2007). Different face parts also receive peak neural representation at unique latencies (Schyns, Petro, & Smith, 2007; Vinette, Gosselin, & Schyns, 2004). Others have suggested that information from faces may be processed hierarchically (Jack, Garrod, & Schyns, 2014), or via a cascade of feature discriminations across time (Florey, Clifford, Dakin, & Mareschal, 2015; Itier, Alain, Sedore, & McIntosh, 2007). Nor are we the first to suggest that the visual system should be equipped to integrate information about face parts across time. For example, Sinha (2011) identified the selection and subsequent storage of information as a key computational challenge in the process of face representation. Likewise, neurophysiological accounts have proposed that perceptual judgments about faces, like gaze direction, may be cumulative, depending on activity that builds across a neural population over time (e.g., Perrett, Oram, & Ashbridge.

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1998). These accounts of integrative face processing are valuable both from a theoretical standpoint, but also from a functional perspective—they suggest a mechanism to provide the perception of faces stability and continuity, an important goal for vision in general (Enns, Lleras, & Moore, 2010; Nijhawan & Khurana, 2010).

It is thus surprising that evidence for emergent representation of faces across time has been mixed. A few investigations appeared to demonstrate that parts of faces can be integrated into a holistic representation of identity across short delays, with the strength of this integration decaying either very rapidly (Singer & Sheinberg, 2006) or up to about half a second later (Anaki, Boyd, & Moscovitch, 2007), but not for longer durations (Farah et al., 1998). These studies suggested that rapid integration occurred primarily via iconic memory, which is known for its high capacity but short-lived storage that decays 150–300 ms after stimulus offset (Brockmole, Wang, & Irwin, 2002; di Lollo, 1980; Irwin & Yeomans, 1986). Anaki et al. (2007) also suggested a possible contribution from visual short-term memory (VSTM), known for having lower capacity, more symbolic content, and slower decay that extends well beyond one second (Brockmole et al., 2002; Irwin & Gordon, 1998; Phillips, 1974). However, a more recent investigation showed that these integration effects with identity could be more easily explained as a byproduct of the composite task used in each design (Cheung, Richler, Phillips, & Gauthier, 2011). In this context, Cheung et al. (2011) showed that previous effects of identity integration were not perceptual in nature, but instead were consistent with response interference when recollecting associations between faces and names. There is thus little unequivocal evidence that the visual system can integrate different pieces of face information into a coherent and emergent representation over time. However, these findings only pertain to the perception of identity in the context of a specific research design—they do not preclude the temporal integration of other kinds of information on a face in different contexts.

Several empirical findings suggest that emergent representation of faces is still reasonable to expect. First, temporal integration appears to be a general feature of information processing, and it occurs across multiple stages of visual representation. For example, judgments of object orientation and numerosity, or even a whole face's identity can be pulled or biased in the direction of a preceding stimulus even several seconds later (Fischer & Whitney, 2014; Liberman, Fischer, & Whitney, 2014). This kind of serial dependence likely serves to promote perceptual stability, and it is consistent with reports that ongoing representation in ventral visual areas is constrained by an object's continuity across space and time (Yi et al., 2008). Second, temporal integration of scenes and objects is supported by multiple visual mechanisms—iconic memory (Brockmole et al., 2002; Irwin & Yeomans, 1986), which includes both visible and informational persistence (di Lollo, 1980; di Lollo & Dixon, 1988), and VSTM (Brockmole et al., 2002; Hollingworth, Hyun, & Zhang, 2005; Irwin, 1993)—either of which could, in theory, support integration of information across face parts over time. Third, viewing a series of partially occluded faces in succession is sufficient to produce facial expression aftereffects (Luo, Wang, Schyns, Kingdom, & Xu, 2015). Crucially, however, the neural pooling that led to this adaptation did not produce enough perceptual integration for observers to recognize the expressions on the adapting faces. It is important to note that pooling information from two intact faces across time (i.e., combining two global percepts, Liberman, Fischer, & Whitney, 2014) or summing activity from fractured faces to influence adaptive coding (e.g., Luo et al., 2015), is different from integrating distinct features across time into a singular metric of facial information. Thus, even though (a) integrative processes are commonplace in visual processing, and (b) other kinds of integrative effects have been shown with face stimuli, there is currently no direct evidence that the process of emergent representation can occur *across* face parts, over time.

We speculated that temporal integration would be especially likely to occur across dynamic facial features, like head and eye rotations, for which changes over time are meaningful and common. Indeed, distinguishing dynamic and invariant facial features has been a central component of theories of face representation (Bruce & Young, 1986), and different populations of ventral visual neurons are known to encode invariant versus changeable aspects of faces, such as identity and gaze direction (Hoffman & Haxby, 2000, although see Pallett & Meng, 2013). As we noted above, accumulation and integration have been identified as central to the ongoing perception of dynamic face parts, in particular (e.g., Perrett et al., 1998; Sinha, 2011). It is thus reasonable that temporal integration may be relatively weak for a stable feature like identity, and it is plausible that emergent integration across time would be more beneficial, and therefore more likely to occur, for the perception of gaze direction. Here, we leverage a powerful demonstration of emergent gaze—the Wollaston effect (Wollaston, 1824; Figure 1), in which gaze direction is perceived as an emergent combination of head and eye rotations—to evaluate whether gaze direction is perceived as an emergent feature when its constituent facial features are seen sequentially instead of simultaneously.

To discriminate another person's direction of gaze, the visual system integrates local pupil information with the rotation of the head (Cline, 1967; Kluttz et al., 2009; Langton et al., 2004; Maruyama & Endo, 1984; Otsuka et al., 2014; Wollaston, 1824). Figure 1 illustrates one example of this phenomenon. Here, the rotations of the pupils and irises 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. A few recent studies examined the mechanisms of this emergent representation of gaze (e.g., Otsuka, Mareschal, & Clifford, 2016; Sweeny & Whitney, 2017), but they only focused on integration across space. Our main goal was to evaluate whether this process of emergent integration also unites information about face parts across time. To accom-

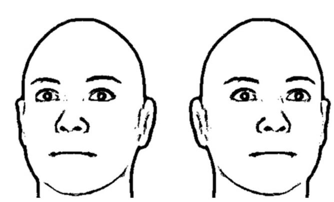

Figure 1. Eyes with identical pupil rotations appear to have unique gaze directions when coupled with leftward or rightward head rotations. In both images, the shapes of the scleras (the white sections of the eyes) and the locations of the irises and pupils within the scleras are identical.

plish this, we evaluated whether the emergent perception of gaze would persist even when a person's face and eyes were seen sequentially. If so, seeing a head rotated to the left (or right) should attract the apparent gaze direction of a pair of pupils seen shortly after, in that same direction. We note that we presented heads and eyes separately as a means to measure the boundaries of temporal integration, and not to test sequential perception per se. In addition to testing this more general hypothesis, we also aimed to examine the temporal boundaries of gaze integration. A central challenge of object processing (e.g., Fischer & Whitney, 2014; Yi et al., 2008) is to determine which features of the environment are related and stable across time, and then afford these objects continuity, both in representation and perception. We predicted that gaze integration would be limited by the strength of object continuity. Specifically, we predicted that attractive effects would (a) weaken when temporal cues indicated that the head and eyes should be regarded as distinct objects, but (b) remain strong in the midst of changes irrelevant to a face's status as a stable object.

In each experiment, observers viewed an image of a head without eyes followed by an image of eyes without a head. On each trial, observers indicated the precise direction in which they perceived the eyes to be looking. Across our experiments, we predicted a general effect of temporal gaze attraction in which the rotation of the head would attract the perceived gaze direction of the eyes seen a moment later. Testing this hypothesis was our main goal. Our second goal was to test how gaze integration might depend on object continuity. In each experiment, we varied the amount of time between the presentation of the head and eyes. Previous work showed that iconic memory and VSTM facilitate relatively stronger and weaker effects of integration across short and long temporal delays, respectively (Brockmole et al., 2002; Hollingworth et al., 2005; Phillips, 1974). We thus expected that integration would be the strongest with shorter delays (e.g., 0 ms) and decay with increasing temporal intervals (e.g., 1,000 ms) between the head and eyes. Additionally, in Experiments 1a and 1b we varied the presentation time of the head with the intent of manipulating the perception of its continuity with the eyes (with longer viewing times possibly even leading to visual adaptation; Kohn, 2007; Rhodes, Jeffery, Clifford, & Leopold, 2007). In these conditions, we predicted that longer exposure to the first cue—the head—would at least diminish or even eliminate the attractive effect on the subsequently presented eyes. In Experiment 2, we examined whether gaze integration across time would persist despite changes in a face's emotional expression. Because facial expressions are inherently dynamic (e.g., Curio, Bülthoff, & Giese, 2011), gaze must often be seen against a backdrop of changing facial musculature. Robust integration of gaze across time should be invariant to these changes. We therefore predicted that gaze attraction would be just as strong when a head and eyes depicted different emotional expressions as when they depicted the same emotion.

Experiment 1a

We conducted Experiment 1a as a preliminary test of the hypothesis that emergent representation of gaze would occur across time, and that this integration would be gated by the temporal continuity between the head and the eyes. We manipulated temporal continuity by (a) varying the delay between the offset of the rotated head and the onset of the test eyes, and (b) presenting the rotated head for a short or long duration. Manipulating the presentation time of the head also allowed us to rule out the possibility that potential attraction effects were driven by integration with an afterimage.

Method

Observers. Thirty undergraduate students from the University of Denver provided consent and participated in Experiment 1. This study was approved by the Institutional Review Board at the University of Denver. Each observer had normal or corrected-to-normal visual acuity and completed the experiment in a dimly lit room. In previous investigations with nearly identical stimuli, sample sizes of eight (Sweeny & Whitney, 2014) and nine (Sweeny & Whitney, 2017) were sufficient to capture a similar effect of emergent gaze when features were presented simultaneously. We expected that this effect might be weaker when features were presented across time, so we more than tripled our sample size for this initial experiment.

Stimuli. To manipulate head and eye rotation independently, we utilized a stimulus set developed for two previous investigations in which our predicted effect of gaze attraction occurred when a head and a pair of eyes were seen simultaneously (Sweeny & Whitney, 2014, 2017). Below, we describe the creation of these faces. We used FaceGen software (FaceGen Modeler, Version 3.5.5; Singular Inversions, Toronto, Ontario, Canada) to create heads with $-8°$ and $+8°$ horizontal rotations (turned toward the observer's left or right, respectively). Next, we used a head with a straightforward rotation (0°) to generate pupils with six rotations around a vertical axis (-25, -15, -5, $+5$, $+15$, and $+25$%). Note that unlike with the head rotations, these values reflect the *percentage*, and not the degrees, of a given pupil's or iris' simulated rotation within the eye opening of a three-dimensional head. A value of zero indicates a direct gaze. A value of $+25$ indicates that, relative to its position when gaze is direct, the outside edge of a given iris has been rotated 25% of the distance to the edge of the eye aperture.[1] 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 we could independently vary the rotations of the head and pupils, while the rotation, size, and shape of the eye aperture

[1] We anticipate that some readers may wish to translate our pupil rotations and 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 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 0.276° of pupil rotation. According to this conversion, the 10-unit steps in our response face reflected fine adjustments of about 2.76°. Although we are confident in this conversion, it is still an estimate, thus we describe our stimuli, analyses, and results in terms of % rotation.

remained fixed. For example, when a +5% eye rotation appeared on a rightward- or leftward-rotated head, the width of the sclera, the shape of the eye aperture, and the placement of the iris and pupil within these features were identical on both faces.

We selected these six pupil rotations based on the results of a separate investigation which showed that unique emergent gaze percepts were strongest when integration occurred between relatively direct head and eye rotations (Sweeny & Whitney, 2017). We also note that the attractive effect from the head we measure here is distinct from a separate effect that emerges from the changing shape of the eye aperture as it shifts on a three-dimensionally rotated head (Anstis, Mayhew, & Morley, 1969; Mareschal, Calder, Dadds, & Clifford, 2013; Otsuka et al., 2014, 2016). For simplicity, we focus here on the attractive effect from the rotation of the head in its more basic form.

We schematized the faces using a three-step process in Adobe Photoshop (Creative Suite 5, Version 12.0). First, we applied a high-pass filter with a 4-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 shading information and it equated all faces in terms of low-level visual information. Each face subtended 2.56° × 2.31° of visual angle.

Procedure. Observers initiated each trial by pressing the space bar, after which a white screen (luminance = 90.13 cd/m^2) with a central fixation point (0.10° of visual angle) immediately appeared and remained visible for the duration of each trial. After a 100-ms blank interval, observers viewed a head rotated to the left (−8°) or right (+8°) for 1 s or 7 s (first box in Figure 2). The rotated head always appeared directly above the fixation point (2.51° from fixation to the center of the face). The test eyes appeared in the same location, where the eyes were missing in the rotated head (see Figure 2). We presented the stimuli at this parafoveal location (Larson & Loschky, 2009) to increase the difficulty of the task and to promote a more globally distributed spread of attention, thereby encouraging observers to attend to the spatial region that contained the head and eyes. We note, however, that our stimuli were still close enough to fixation to allow for detailed processing of the head and eyes, and integration into an emergent percept (Florey et al., 2015; Palanica & Itier, 2015).

Next, observers viewed a pair of eyes with one of six amounts of pupil rotation (−25, −15, −5, +5, +15, and + 25%; second box of Figure 2) for 150 ms. The onset of these test eyes was separated from the offset of the rotated head by delays of 0, 500, or 1,000 ms. We selected these interstimulus intervals (ISIs) as an initial test of how potential effects of attraction might decay over time, which would allow us to make inferences about the extent to which gaze integration may depend on different mechanisms of visual memory. For example, strong integration via iconic memory (and informational persistence, in particular) extends up to 150–300 ms after stimulus offset (e.g., Brockmole et al., 2002; di Lollo, 1980; Irwin & Yeomans, 1986), whereas weaker integration is known to occur in VSTM starting around 500 ms and at least up to 1,000 ms after stimulus offset (Brockmole et al., 2002; Hollingworth et al., 2005).[2]

All of the test eyes were immediately followed by a mask, shown for 100 ms (see the third box in Figure 2). Masks were generated by taking the same image of four rotated and overlapping faces, then breaking this image up into 80 squares and randomly reshuffling them into a new image. A random shuffling procedure produced a new mask on each trial. A 1,000-ms delay followed the offset of the mask, after which observers viewed a response face with a full combination of head contours, internal features, and eyes (see the fourth box of Figure 2). We selected a full face rather than a pair of isolated eyes as the response stimulus for a few reasons. First, a full response face was an effective response stimulus in a similar task with these same stimuli (Sweeny & Whitney, 2014, 2017). Second, and more importantly, even though a pair of isolated response eyes still provide useful data for measuring gaze perception, they tend to compress the range of reported gazes relative to a pair of eyes within a head (Sweeny & Whitney, 2017). Observers were instructed to adjust the pupils on the response face to match the gaze direction of the previously seen test eyes (but not the rotated head) using the left and right arrows on a keypad. Observers were encouraged to be precise and were given unlimited time to respond. The response face always had straightforward features (the head had 0° of horizontal rotation). Only the pupil positions could be rotated, in 10% increments between −95% and +95% (we used the same approach for creating these response faces as with the test faces and eyes described earlier). The starting pupil rotation on the response face was randomly selected on each trial from a uniform distribution between −95% and +95%. The response face was superimposed with its center on the fixation point so that adjustments of its eyes were not based on exact spatial correspondence with the test eyes. The response face remained on the screen until the observer pressed the space bar.[3]

Twenty-three observers completed a total of 288 trials and seven observers completed a total of 144 trials (due to time constraints). All stimuli were presented on a 16-in. CRT monitor with a refresh rate of 85 Hz.[4] Observers sat at a viewing distance of 57 cm.

Results

Does emergent gaze perception occur across time? The primary goal of this investigation was to determine whether head rotation influenced the perceived gaze of a pair of eyes seen a moment later. We also sought to verify that observers still used information from the eyes to inform their gaze judgments, above and beyond any influence from the head. To accomplish these objectives, we calculated the average perceived gaze associated with each of the six pupil rotations on the test eyes, separately for

[2] We presented a pattern mask after the offset of the head on 40% of trials in this preliminary experiment. Masking did not influence our results, consistent with a contribution from visual short-term memory (which is not disrupted by masking; Phillips, 1974). However, it is difficult to rule out the possibility that this null effect was simply because our masks were ineffective. We thus present data only from the trials without masking.

[3] We did not record response times in Experiments 1a and 1b. However, we conducted an additional pilot experiment ($N = 11$) with similar presentation parameters to get a sense for how long it may have taken observers to respond in the experiments in this investigation. On average, observers took 2.15 s ($SD = 0.66$) to complete the adjustment procedure (after separately rejecting outliers beyond each observer's mean reaction time (RT) ±2.5 *SD*s).

[4] Because of the 85-Hz refresh rate of the monitor, the presentations of the mask and test eyes lasted 106 ms and 153 ms, respectively. The presentation durations of the rotated head also varied slightly from the durations of 1 or 7 s, as listed in the figures. We refer to the approximate times throughout the manuscript for ease of presentation.

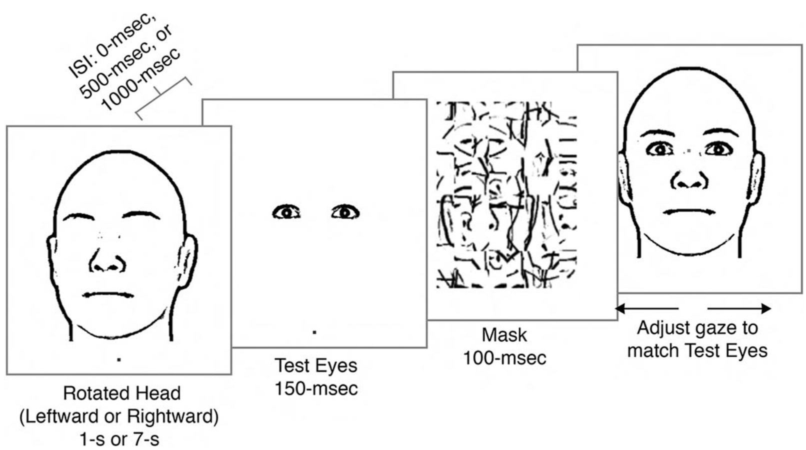

Figure 2. A leftward- or a rightward-rotated head was presented on the screen for 1 s or 7 s. After an interstimulus interval (ISI) of 0, 500, or 1,000 ms, a pair of leftward- or rightward-rotated test eyes then appeared on the screen for 150 ms. The test eyes were immediately followed by a 100-ms scrambled mask. Observers then adjusted the pupil rotation on the response face to match the perceived gaze direction of the test eyes.

each observer. We did this separately for trials with leftward-rotated and rightward-rotated heads, with data collapsed across the ISIs and head durations (we evaluate effects of timing on gaze judgments later). We then conducted a repeated-measures analysis of variance (ANOVA) with factors of head rotation (leftward and rightward) and pupil rotation (−25, −15, −5, +5, +15, and + 25%). As we expected, this ANOVA revealed a main effect of head rotation, $F(1, 29) = 6.19$, $p = .02$, $\eta_p^2 = 0.18$, a main effect of pupil rotation, $F(5, 145) = 49.33$, $p < .001$, $\eta_p^2 = 0.63$, and no interaction between head and pupil rotation, $F(5, 145) = 0.47$, $p = .80$, $\eta_p^2 = 0.02$. The main effect of head rotation confirmed that the perceived gaze of a pair of eyes was pulled in the direction of a rotated head seen a moment earlier (Figure 3a). The main effect of pupil rotation indicated that physical eye rotation did influence gaze judgments, *independent* of any influence from the head. That is, observers did not simply make coarse right-left judgments based on the rotation of the head alone.

As an additional test of sensitivity to eye gaze, we calculated the slope of the relationship between physical pupil rotation and perceived gaze for each observer, with data collapsed across the two head rotations. This analysis was designed to reveal just how much pupil rotations influenced gaze judgments, beyond the main effect described above. Perfect perception of gaze would produce a slope of 1. With an average slope of 0.82, observers in Experiment 1a were indeed sensitive to the rotation of the pupils (compared against a slope of 0 with a one-sample t test: $t(29) = 2.76$, $p = .001$, $d = 0.51$), albeit with a nonsignificant tendency for underestimation (compared against a slope of 1.0: $t(29) = 0.59$, *ns*). With these primary effects clearly indicating that the emergent perception of gaze does

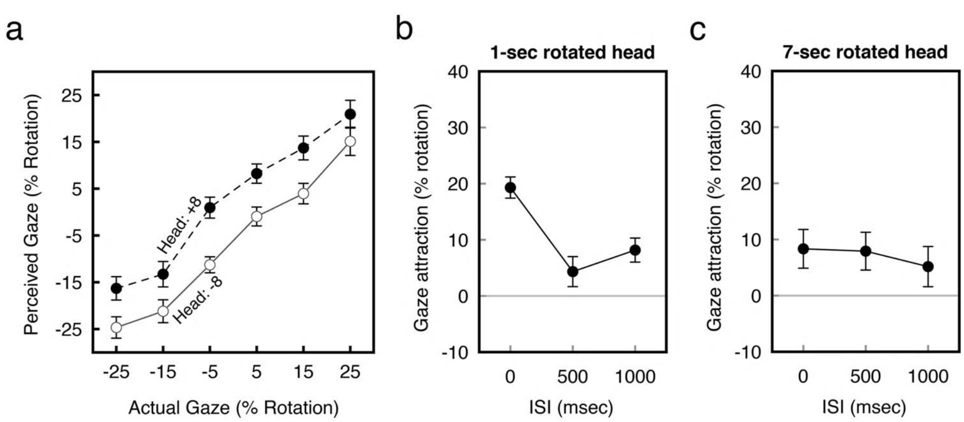

Figure 3. Effects of emergent gaze across time in Experiment 1a. The relationship between perceived gaze and physical pupil rotation plotted separately for leftward and rightward head rotations, with data collapsed across interstimulus intervals (ISIs) and head durations (a). Attraction scores are shown separately for trials in which observers viewed a rotated head for (b) 1 s or (c) 7 s, and as a function of the delay (ISI) between the offset of the rotated head and the onset of the test eyes. Error bars in each panel represent ±1 *SEM*, adjusted for within-observer comparisons within each series of connected data points.

indeed occur across time, we now move on to discuss the temporal dynamics of this process.

Gaze attraction index. In order to facilitate our analysis of the temporal dynamics of emergent gaze, we created an attraction index to quantify the extent to which head rotations influenced the perceived gaze of the test eyes. We used this attraction index as the dependent variable in each of the analyses reported below. This index reflected the difference between the perceived gaze of eyes that followed a rightward-rotated head (+8°) and the perceived gaze of eyes that followed a leftward-rotated head (−8°). Having already determined that observers were sensitive to local information about pupil rotations (see above), we collapsed data across the six pupil rotations of the test eyes when computing this index. In this index, positive and negative values indicated that perceived gaze had been attracted toward, or repelled from, the direction of the head rotation, respectively. For example, collapsed across the different ISIs and head durations in the unmasked condition, Observer 1 indicated that the test eyes appeared to be rotated to the left (−13.3%) when they followed a leftward-rotated head, and to the right (+13.6%) when they followed a rightward-rotated head. The difference between these two scores (an attraction score of +26.94%) indicates that, at least for this observer, the same sets of eyes appeared to gaze in different directions simply by virtue of being seen after differently rotated heads. Half of the attraction index indicates the amount of gaze attraction from one 8°-rotated head for this observer (13.47%; or ~3.72° based on our conversion of % rotation to degrees; see Footnote 1).

What are the temporal dynamics of emergent gaze perception? Our next objective was to evaluate how the integration of information from the head and eyes depended on the extent to which these features were separated in time. We conducted a repeated-measures ANOVA to assess the individual and combined effects of ISI (0, 500, and 1,000 ms) and head duration (1 s and 7 s) on the perception of gaze using the attraction index as our dependent variable. This ANOVA revealed a main effect of ISI, $F(2, 58) = 4.56$, $p = .01$, $\eta_p^2 = 0.09$, but no main effect of head duration, $F(1, 29) = 1.77$, $p = .19$, $\eta_p^2 = 0.06$, and no interaction between ISI and head duration, $F(2, 58) = 2.65$, $p = .08$, $\eta_p^2 = 0.11$.

We can draw a few conclusions from Experiment 1a. First, and most importantly, the human visual system appears to be capable of integrating information about gaze direction from multiple features across time. Second, the strength of integration may depend on the extent to which face parts are seen as belonging to a continuous and unified object, as integration effects were strongest when the eyes were seen immediately after the head (see Figure 3b). This pattern of weakening temporal integration resembled the decay rate of visual memory (e.g., Phillips, 1974), with the strongest integration after the 0-ms ISI likely reflecting an effect of iconic memory, and informational persistence in particular (e.g., di Lollo & Dixon, 1988).

Experiment 1a also produced some intriguing patterns that deserve further exploration. The pattern of decaying integration across long ISIs tended to be strongest when the head was seen for just a second, reflected by a trending interaction in a repeated-measures ANOVA (see above). Fischer and Whitney (2014) described a similar kind of weakening in the serial dependence of orientation perception, which they framed as evidence of ongoing competition between integrative and repulsive/adaptive-coding mechanisms. We suspect that some of our subtle effects of gaze integration would have been more stable had observers completed more trials—an issue we address next, in Experiment 1b. Nevertheless, these data allow us to rule out the possibility that the integration effects in Experiment 1a occurred via fusion of the test eyes with an afterimage from the rotated head, an important consideration when studying effects of visual memory (Sligte, Scholte, & Lamme, 2008). If this were the case, integration would have been stronger after viewing the rotated head for the longer duration since this would have produced a stronger afterimage; yet we found the opposite pattern.

Experiment 1b

The exploratory data in Experiment 1a were noisier than we had anticipated. In Experiment 1b, we aimed to replicate our main findings of gaze integration, and then gather additional evidence regarding our hypothesis that disrupting the temporal continuity between the head and eyes would weaken gaze integration.

In Experiment 1b, we ran the same conditions from Experiment 1a again with all three ISIs (0, 500, and 1,000 ms) and both head durations (1 s and 7 s). We also included a condition in which the rotated head was presented for 0.1 s. We predicted that effects of gaze attraction would be especially strong with this very brief head duration, and that they would weaken with the longer head durations. Using a 0.1-s rotated head also allowed us to measure a potential contribution of sensory persistence on the perception of emergent gaze. Unlike informational persistence, which is time-locked to the *offset* of an image and persists even after an image is no longer seen (di Lollo & Dixon, 1988), visible persistence is known to last approximately 100 ms after the *onset* of an image (e.g., di Lollo, 1980), and is characterized by the experience of seeing an object after its physical termination. Accordingly, the head and eyes in this experiment could have reasonably been expected to appear to have been simultaneously present (or nearly so) when the eyes appeared immediately after such a briefly presented head (i.e., the 0-ms ISI paired with the 0.1-s adaptation).

Method

Observers. Thirty observers provided consent and participated in Experiment 1b. Each observer had normal or corrected-to-normal visual acuity.

Stimuli and procedure. The stimuli and procedures were identical to those in Experiment 1a, except that (a) an additional condition was added in which the rotated head appeared for 0.1 s, and (b) each observer completed 24 rather than 12 trials of each condition. Each observer completed 432 trials.

Results

Does emergent gaze perception occur across time? As in Experiment 1a, we first evaluated the contributions of head rotation and physical pupil rotation on perceived gaze, independent of the temporal dynamics of integration. As before, we observed a main effect of head rotation, $F(1, 31) = 6.60$, $p = .006$, $\eta_p^2 = 0.17$, a main effect of pupil rotation, $F(5, 155) = 58.13$, $p < .001$, $\eta_p^2 = 0.65$, and no interaction between head and pupil rotations, $F(5, 155) = 1.64$, $p = .15$, $\eta_p^2 = 0.05$. The main effect of head rotation and the main effect of pupil rotation indicate that each feature independently influenced the reports of gaze direction. Additionally, we quantified the extent to which observers were using information from the eyes to guide their responses by calculating the slope of the relationship between the physical pupil rotation and perceived gaze, collapsing across the two head rotations. With an average slope of 0.97, observers were very sensitive to the rotation of the pupils (compared against a slope of zero using a one-sample *t* test: $t(29) = 6.27$, $p = .001$, $d = 1.14$). Thus, any influence of head rotation on perceived gaze in the analyses below would occur over and above this sensitivity to eye gaze.

What are the temporal dynamics of emergent gaze perception? As in Experiment 1a, we calculated the attraction index to evaluate the temporal dynamics of emergent gaze perception. We conducted a repeated-measures ANOVA to assess the individual and combined effects of ISI (0, 500, and 1,000 ms) and head duration (0.1, 1, and 7 s) on integration of gaze direction over time. This analysis revealed a main effect of ISI, $F(2, 58) = 18.80$, $p < .001$, $\eta_p^2 = 0.39$, a main effect of head duration, $F(2, 58) = 5.24$, $p = .008$, $\eta_p^2 = 0.15$, and an interaction between ISI and head duration, $F(4, 116) = 2.74$, $p = .03$, $\eta_p^2 = 0.09$.

We more deeply assessed the extent to which timing influenced the strength of gaze integration by conducting planned paired-samples *t* tests. Effect sizes for within-subject comparisons here and in subsequent analyses were corrected for dependence among means (Morris & DeShon, 2002). Planned paired-samples *t* tests revealed that the predicted effect of decaying attraction with the longer ISIs occurred more reliably with the briefest head durations. When the rotated head was seen for just 0.1 s, attraction was stronger with the 0-ms ISI compared with both the 500-ms ISI, $t(29) = 4.08$, $p = .0003$, $d = 0.77$, and the 1,000-ms ISI, $t(29) = 3.50$, $p = .002$, $d = 0.64$, but there was no difference in attraction between the 500-ms and 1,000-ms ISIs, $t(29) = 0.77$, $p = .45$ $d = 0.13$ (Figure 4a). When the head was seen for 1 s, attraction was stronger with the 0-ms ISI compared with both the 500-ms ISI, $t(29) = 3.98$, $p = .0004$, $d = 0.74$, and the 1,000-ms ISI, $t(29) = 4.43$, $p = .0001$, $d = 0.82$, but again there was no difference in attraction between the 500-ms and 1,000-ms ISIs, $t(29) = 0.77$, $p = .43$, $d = 0.08$ (Figure 4b). When the head was seen for 7 s, we observed stronger attraction with the 0-ms ISI compared with the 500-ms ISI, $t(29) = 3.38$, $p = .002$, $d = 0.62$, but not compared with the 1,000-ms ISI, $t(29) = 1.74$, $p = .09$, $d = 0.32$. Unlike with the shorter adapter durations, attraction was stronger with the 1,000-ms ISI compared with the 500-ms ISI following the 7-s head, $t(29) = 2.34$, $p = .03$, $d = 0.44$ (Figure 4c). There is some precedence for rebound effects like this—previous work showed that pattern integration via VSTM builds in strength within this time frame (Brockmole et al., 2002; Hollingworth et al., 2005)—although this did not occur consistently throughout our investigation. Despite this general decay over time, one-sample *t* tests confirmed that attraction effects were still greater than zero even after the 1,000-ms ISI (after the 0.1-s head, $t(29) = 3.45$, $p = .001$, $d = 0.63$, after the 1-s head, $t(29) = 2.41$, $p = .02$, $d = 0.44$, and after the 7-s head, $t(29) = 2.80$, $p = .008$ $d = 0.51$).

Overall, these data support our main hypothesis that the visual system can integrate parts of a face seen separately across time into an emergent percept of gaze. This integration persisted, albeit to a weakened extent, after delays of up to one second. The weakening of these integration effects resembles the decay rate of visual memory (e.g., Phillips, 1974), with stronger initial integration via iconic memory and generally weaker integration at longer ISIs presumably via VSTM (e.g., Brockmole et al., 2002; di Lollo, 1980; Phillips, 1974). It is also possible that when eyes were seen immediately after the briefest presentation of the face (the 0-s ISI following the 0.1-s head), observers may have seen a fusion of the head and the eyes, in which case integration could be reasonably attributed to visible persistence (e.g., di Lollo, 1980). Finally, similar to serial dependence in orientation perception (Fischer & Whitney, 2014), we found that viewing the rotated head for a longer duration weakened the overall effect of attraction.

Experiment 2

Experiment 1 provided evidence that disruptions of temporal continuity weaken the emergent integration of gaze. Yet the fact that gaze attraction still occurred across long delays suggests that the visual system prioritizes some invariance to changing contexts

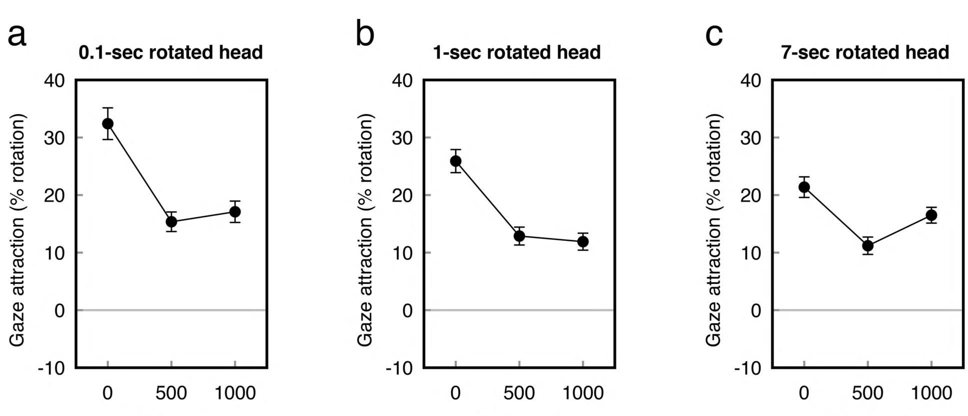

Figure 4. Effects of head rotation on perceived gaze in Experiment 1b. Attraction scores are shown separately for trials in which observers viewed a rotated head for (a) 0.1 s, (b) 1 s, or (c) 7 s, and as a function of the delay (interstimulus interval [ISI]) between the offset of the head and the onset of the test eyes. Error bars represent ±1 *SEM*, adjusted for within-observer comparisons within each series of connected data points.

in pursuit of stable perception of facial information. In Experiment 2 we hoped to push the limits of this invariance, evaluating whether the temporal integration of emergent gaze persists despite a salient and socially relevant source of change—emotional expression. Unlike identity or gender (Pallett & Meng, 2013), facial expressions and gaze are both dynamic. Gaze is also often seen in the context of facial expression of emotion. Changes in gaze can thus be seen on top of stable emotional expressions, and consistent gaze cues can be seen against a backdrop of changing emotion. For gaze perception to be adaptive, the visual system should be able to integrate gaze-related cues across time despite changes in emotional expression. Thus, we expected that integration of emergent gaze would persist even when a rotated head and eyes were seen across changing emotional expressions. For example, the rotation of a head with an angry expression should attract the perceived gaze of a pair of eyes taken from a happy face to the same extent as a head and eyes depicting the same emotion.

Another goal of this experiment was to more precisely characterize the temporal decay of gaze integration. We introduced two new ISIs—100 ms and 2,000 ms—between the presentation of the head and the eyes. These new intervals allowed us to observe the decay of gaze attraction across time with greater precision and range than in the previous experiments. We selected the 100-ms ISI to provide additional information about integration via iconic memory, which has been shown to operate up to 300 ms (Irwin & Yeomans, 1986). We selected the 2,000-ms ISI to examine whether integration effects were robust even beyond 1,000-ms delays. Because VSTM has been shown to operate beyond one second (Brockmole et al., 2002; Irwin & Gordon, 1998; Phillips, 1974), and because effects of serial dependence in the perception of orientation and identity have been shown to last up to 10 s (Fischer & Whitney, 2014; Liberman et al., 2014), we predicted integration effects would persist even after a 2,000-ms delay, albeit to a weaker extent.

Method

Observers. Fifty-seven observers provided consent and participated in Experiment 2. Because we predicted that emotional expressions would not influence the strength of gaze attraction (essentially a null result), we aimed to double our sample size relative to the previous experiments to guard against the possibility of missing such an effect if it were present, but extremely subtle. Each observer had normal or corrected-to-normal visual acuity.

Stimuli and procedure. Stimuli and procedures for Experiment 2 were identical to those from Experiment 1b with the exception of the following changes. We created a new set of stimuli to include faces depicting neutral, happy, and angry facial expressions (Figure 5). We created the stimuli using FaceGen software exactly as described in Experiment 1, including the same head and pupil rotations, except that we adjusted the intensity of the emotional expressions to 100% strength. Although these faces were artificial, their emotional expressions were composite averages based on parameters from hundreds of three-dimensional faces of actual men and women. We were thus confident that the faces in Experiment 2 depicted recognizable and valid expressions of happiness and anger. To create the rotated heads, we removed the eyes and the visual information immediately surrounding them, leaving only the outer contours of the head, ears, and neck, and the contours of the mouth, nose, and eyebrows. To create the test eyes, we extracted each pair of rotated eyes, including the immediately surrounding emotional information (e.g., wrinkles around the eyes) from a straightforward head. This extraction included the iris, sclera, surrounding eye contours, and skin information (to conserve emotionally relevant information near the eyes), and it "erased" all surrounding contours and line information (i.e., head, mouth, nose, and eyebrow outlines). Each face subtended 2.56° × 2.31° of visual angle.

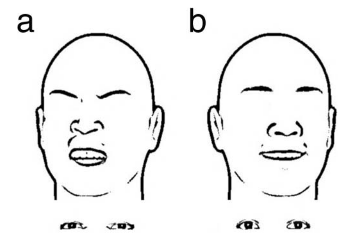

Figure 5. Experiment 2 included faces with neutral, angry, and happy emotional expressions. The heads and eyes from these faces were presented sequentially. Decoupled heads and eyes are shown for (a) an angry face and (b) a happy face.

Procedures were identical to those from Experiment 1, except that there was only one head duration of 0.1 s across all trials, and two additional ISIs were included: 100 ms and 2,000 ms. Trials were counterbalanced so that every combination of head rotation (−8° or +8°), head emotion (neutral, happy, angry), test eye pupil rotation (−25, −15, −5, +5, +15%, and +25%), test eye emotion (neutral, happy, angry), and ISI (0, 100, 500, 1,000, or 2,000 ms) was observed equally. Crossing the expressions on the heads and eyes produced three pairs of possible head-eye combinations on congruent trials (neutral-neutral, happy-happy, and angry-angry) and six pairs of possible head-eye combinations on incongruent trials (neutral-happy, neutral-angry, happy-neutral, happy-angry, angry-neutral, angry-happy). The response face and eyes always displayed a neutral expression, as in the previous experiments. Trials were randomized for each observer, and each observer completed a total of 540 trials.

Results

Does emergent gaze perception occur across time? As in Experiments 1a and 1b, we sought to evaluate the impact of head rotation and physical pupil rotation on perceived gaze regardless of the time differences between the two features, and with data collapsed across the different emotion conditions. A repeated-measures ANOVA revealed a main effect of head rotation, $F(1, 55) = 33.21$, $p < .001$, $\eta_p^2 = 0.38$, a main effect of pupil rotation, $F(5, 275) = 40.15$, $p < .001$, $\eta_p^2 = 0.42$, and an interaction between head and pupil rotations, $F(5, 155) = 3.38$, $p = .006$, $\eta_p^2 = 0.098$. Additionally, we evaluated the relationship between the physical pupil rotation and the perceived gaze, and found that with a slope of 0.61, observers were sensitive to the rotation of pupils (compared against a slope of zero with a one-sample t test: $t(56) = 3.02$, $p = .004$, $d = 0.40$, but with a nonsignificant tendency for underestimation (compared against a slope of 1.0: $t(56) = 1.97$, $p = .05$, $d = 0.26$).

What are the temporal dynamics of emergent gaze perception on emotional faces? Using the attraction index, we conducted a repeated-measures ANOVA to assess the individual and combined effects of ISI (0, 100, 500, 1,000, and 2,000 ms) expression on the head (neutral, happy, angry), and expression on the eyes (neutral, happy, angry). This analysis revealed a main effect of ISI, $F(4, 220) = 3.66$, $p = .007$, $\eta_p^2 = 0.21$, but no main effects of Expression on the Head, $F(2, 110) = 0.37$, $p = .69$, $\eta_p^2 = 0.01$, or Expression on the test Eyes, $F(2, 110) = 0.19$, $p = .82$, $\eta_p^2 = 0.004$. None of the interactions were significant: ISI × Expression on the Head; $F(8, 440) = 0.96$, $p = .46$, $\eta_p^2 = 0.02$, ISI × Expression on the Eyes; $F(8, 440) = 0.88$, $p = .54$, $\eta_p^2 = 0.02$, Expression on the Head × Expression on the Eyes; $F(4, 220) = 0.13$, $p = .97$, $\eta_p^2 = 0.001$, or ISI × Expressions on the Head and Eyes; $F(16, 880) = 0.50$, $p = .95$, $\eta_p^2 = 0.01$. The main effect of ISI provides additional evidence that gaze attraction decayed across increasing temporal delays. Perhaps most importantly for this particular experiment, the lack of an interaction between the expressions on the heads and eyes suggests that the congruity of a person's emotional expression across time had no influence on the strength of gaze integration (Figure 6a is a depiction of gaze attraction as a function of congruency across the 5 ISIs).

We conducted planned paired-samples *t* tests to evaluate the general strength of attraction across the different ISIs using data collapsed across the emotional expressions on the heads and eyes. The predicted effect of decaying attraction occurred after the longest ISI of 2,000 ms compared with each of the other ISIs. Attraction was weaker with the 2,000-ms ISI compared with the 0-ms ISI, $t(56) = 2.62$, $p = .01$, $d = 0.37$, the 100-ms ISI, $t(56) = 2.09$, $p = .04$, $d = 0.31$, the 500-ms ISI, $t(56) = 4.32$, $p < .001$, $d = 0.58$, and the 1,000-ms ISI, $t(56) = 3.36$, $p = .001$, $d = 0.45$. There were no statistically significant differences in attraction between any of the shorter ISIs (*p* values ranged from 0.069 and 0.803). Gaze attraction was significantly greater than zero even with the longest ISI (2,000 ms), $t(56) = 4.79$, $p < .001$, $d = 0.64$.

General and specific effects of emotional expression on gaze perception. Emotional expressions are powerful visual cues. In fact, the perception of emotional expression is known to influence the perception of gaze and vice versa (Adams & Kleck, 2005; Lobmaier, Tiddeman, & Perrett, 2008). We thus conducted an exploratory analysis to evaluate a general effect of emotional expression on gaze attraction. We evaluated whether or not the increased salience of emotional expressions boosted the strength of gaze attraction compared with that from neutral expressions. For simplicity, we focused this analysis specifically on trials in which the heads and eyes conveyed congruent facial expressions. There were no statistically significant differences in the strength of gaze attraction between trials with neutral and emotional facial expressions, collapsed across ISIs, $t(56) = 0.059$, $p = .953$, $d = 0.008$ (Figure 6b). Thus, an emotional visual context produced no measurable increase in the strength of gaze attraction. An additional exploratory analysis of effects from specific emotional expressions on gaze discrimination can be found in the supplemental materials available online.

To summarize, in Experiment 2 we tested the resilience of gaze attraction by introducing a dynamic emotional context, which, unlike displacement in time, should not have threatened the face's perceived continuity. We found that gaze attraction persisted despite salient but task-irrelevant emotional expressions on the faces. These integrative effects were even robust to changes in the emotional content of the head and the subsequently presented eyes. Furthermore, while there was decay in the strength of gaze attraction over time, integration nonetheless occurred even at longer delays of 2 s. Overall, these findings provide insight into the strength and persistence of integration in the emergent perception of gaze.

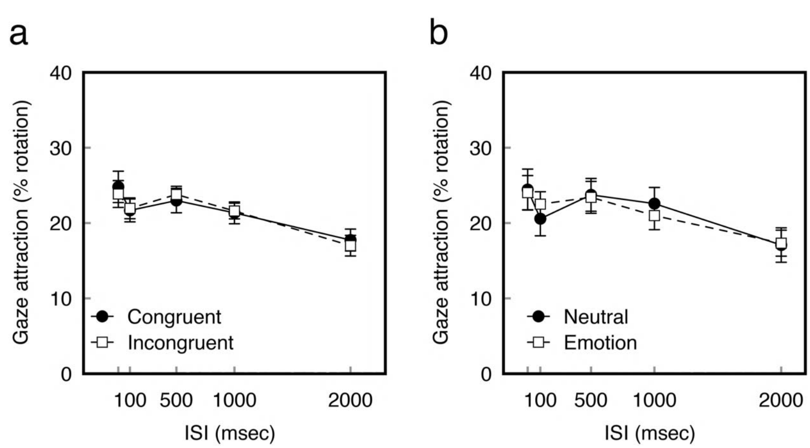

Figure 6. Effects of head rotation on perceived gaze in Experiment 2. (a) Attraction scores are shown separately for trials in which observers viewed heads and eyes that displayed either congruent or incongruent emotional information. (b) Attraction scores are shown separately for trials in which the heads and eyes displayed either neutral or emotional information. In both panels, attraction scores are shown as a function of the delay (interstimulus interval [ISI]) between the offset of the head and the onset of the test eyes. Error bars represent ±1 *SEM*, adjusted for within-observer comparisons within each series of connected data points.

Discussion

We showed that emergent perception of gaze occurs across time. Specifically, when a rotated head and a pair of eyes were seen in succession, the visual system integrated these features, pulling the perceived gaze of the eyes toward the rotation of the head. Across multiple experiments we revealed that this integrative process is constrained by temporal boundaries of object continuity; gaze attraction decayed with increasing temporal distinction between the head and the eyes. We also showed that despite this limitation, the visual system is surprisingly flexible in its representation of faces over time; information from a head and eyes was still integrated even after delays of up to two seconds and gaze attraction was invariant to changing emotional content on the face. In other words, this process does not appear to act indiscriminately. Rather, it appears to engage to the extent that features seem to belong together. Yet it may also serve to further stabilize and promote object continuity, an important outcome for vision in general (Fischer & Whitney, 2014; Yi et al., 2008).

The current findings are important for several reasons. First, they add temporal constraints to a growing understanding of how the visual system builds emergent representation of gaze (Cline, 1967; Kluttz et al., 2009; Langton et al., 2004; Maruyama & Endo, 1984; Otsuka et al., 2014, 2016; Perrett, Hietanen, Oram, Benson, & Rolls, 1992; Wollaston, 1824). Second, they converge with recent evidence to suggest that visual integration may be especially strong with regard to dynamic facial cues (Luo et al., 2015). Favelle, Tobin, Piepers, Burke, and Robbins (2015) showed that dynamic faces are processed holistically. This implies either that multiple, distinct holistic representations would need to be created separately and then integrated across time, that information about different parts could group and accumulate across time, or both. Our results provide evidence for the second interpretation. Our work demonstrates that temporal integration is not limited to repeated presentations of fully intact faces (Fischer & Whitney, 2014; Liberman et al., 2014), but also occurs across distinct parts. Third, our work highlights the value of information accumulation and storage in understanding face representation (Perrett et al., 1998; Sinha, 2011), in this case demonstrating a perceptual consequence of these general visual processes.

We want to emphasize that we presented heads and eyes separately primarily as a means to measure the process of integration, not sequential perception of face parts per se. Nevertheless, the integration we have shown here could also be used to support perception on occasions when face parts are seen separately. For example, when a face seen in the periphery is brought into foveal or parafoveal vision, in which case head rotation could be discriminated before that of the eyes (e.g., Florey et al., 2015; Palanica & Itier, 2015). Temporal integration could also be valuable when a person is seen first with closed eyes, and then with open eyes, or as others have suggested, when a shadow or unusual lighting moves across a person's face and eyes (Perrett et al., 1992).

Decades of work have shown that the visual system represents faces at an emergent level, integrating information across space so that they are perceived as unified wholes rather than disconnected parts (e.g., Farah et al., 1998; Suzuki & Cavanagh, 1995). Despite an abundance of attention and demonstrations of flexibility across feature domains (e.g., race; Michel, Rossion, Han, Chung, & Caldara, 2006; emotion; Sweeny, Suzuki, Grabowecky, & Paller, 2013; and gaze; Wollaston, 1824), it has been surprisingly difficult to determine whether integration of face parts also extends across time (Anaki et al., 2007; Cheung et al., 2011; Singer & Sheinberg, 2006) and at a perceptual rather than a cognitive level. The current results, however, are perceptual and do not stem from decision-related interference (Cheung et al., 2011) or response bias. Had our observers simply adopted a strategy of providing responses consistent with the rotation of the head, then prolonged exposure to the head should have caused an increase rather than a reduction in attraction effects, and the delay between the head and the eyes would have been unlikely to influence the strength of integration. To further rule out response bias, we ran an additional experiment (see the supplemental materials available online) in which we presented heads and eyes at the same spatial location or in different locations. If observers based their responses solely on the rotation of the head, then attraction would have occurred regardless of spatial discontinuity. Instead, we found our effect of gaze attraction only when the head and eyes appeared in the same location. Gaze attraction was also not due to integration of the eyes with an afterimage of the head. If this were the case, attraction would have been stronger, not weaker, after prolonged viewing of the rotated head. The current results thus bridge an important gap in understanding a key visual mechanism for stabilizing the perception of social information across time.

Our findings bear at least a superficial resemblance to other notable effects of perceptual attraction over time. For example, in a phenomenon known as representational momentum, an object's perceived orientation is attracted to the implied motion direction of a similar object seen a moment earlier, and the strength of this attraction decays up to 750 ms (Freyd & Finke, 1984). Similarly, in the feature inheritance effect, the offset of a single vernier can be integrated into the global appearance of a larger grating (Herzog & Koch, 2001). Unlike our effect, this kind of inheritance occurs on an extremely fast time scale, and only when the first feature is not perceived. Finally, in a phenomenon known as serial dependence, orientation and even identity judgments are biased in the direction of a similar object seen up to 10 s earlier (Fischer & Whitney, 2014; Liberman et al., 2014). This kind of attraction may be obligatory and reliant on VSTM (Dubé, Zhou, Kahana, & Sekuler, 2014). Although it is unclear to what extent these phenomena and the effect of gaze attraction we found here might rely on shared mechanisms, they nonetheless converge to illustrate the importance of integration across a variety of visual features and temporal delays.

Visual memory is typically regarded as the preservation of visual information after the optical source of that information has disappeared (Palmer, 1999). According to this framework, our effects of gaze attraction can be interpreted as reflecting online integration of information from a pair of eyes with a lingering representation of head rotation maintained in visual memory. We observed some variability across our experiments in terms of the extent to which this integration decayed across time. Yet collectively, these experiments converge on a common theme; gaze attraction tended to become weaker with longer delays. This general pattern of gradual decay bears a notable resemblance to the temporal characteristics of storage and integration associated with distinct types of visual memory. First, we observed the strongest integration with shorter delays between the offset of the head and the onset of the eyes. In just one case, this integration might have occurred via visible persistence, a type of iconic memory that would have fused the head and eyes into a unitary percept (di Lollo, 1980; di Lollo & Dixon, 1988). For the most part, however, these attraction effects were consistent with strong and rapid integration known to occur via informational persistence, another type of iconic memory that decays rapidly up to about 150 ms (Brockmole et al., 2002; di Lollo, 1980) or even 300-msec after stimulus offset (Irwin & Yeomans, 1986). Second, we found that gaze attraction persisted across delays of up to two seconds, albeit to a weakened extent. The pattern of temporal decay we observed over longer delays is at least consistent with the characteristics of (a) VSTM, a slowly decaying lower-capacity system (Phillips, 1974), and (b) a more recently documented higher-capacity memory store known as fragile VSTM, which lasts up to one second (Sligte et al., 2008; Vandenbroucke, Sligte, & Lamme, 2011). Drawing direct comparisons between these findings and our results can be challenging, especially since most examinations of visual memory examine change detection, maintenance of visual information, or capacity, none of which was the focus of our investigation. Future research should more directly evaluate the relationship of these visual mechanisms to the temporal integration of facial features, disentangling what we consider probable contributions from iconic memory and VSTM.

When evaluating the perception of multiple visual features separated by time, it is important to consider possible effects of adaption, even when the net perceptual effect is attractive. Indeed, Fischer and Whitney (2014) proposed that serial dependence in the perception of orientation—an attractive effect at least superficially similar to our own—occurs in spite of ongoing and opposing repulsive effects of visual adaptation. Below, we evaluate the likelihood that similar processes may have been at work in the current investigation. Aftereffects are certainly known to occur both for the perception of gaze direction (Bi, Su, Chen, & Fang, 2009; Jenkins, Beaver, & Calder, 2006) and head rotation (Fang & He, 2005). In fact, head rotation aftereffects can occur after relatively brief adapter durations of 2 and 5 s (Fang & He, 2005), much like the rotated head durations in Experiments 1 and 2. Critically, aftereffects are also known to occur across visual features. For example, adapting to a female body can make an androgynous face appear more masculine (Ghuman, McDaniel, & Martin, 2010). It is plausible that this kind of cross-category adaptation could have occurred between the heads and eyes in the current investigation. Specifically, populations of cells in the macaque superior temporal sulcus 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, Viola, & McCarthy, 2004; Puce, Allison, Bentin, Gore, & McCarthy, 1998). It is therefore possible that, when viewed for increasing amounts of time, the rotated heads (without eyes) in our experiments could have inadvertently adapted the representations of corresponding pupil rotations. Such cross-category adaptation could have subsequently diminished the strength of gaze attraction on the test eyes seen a moment later, a result that is at least consistent with our finding that integration was weaker when heads were viewed for longer durations. We cannot confirm that adaptation played a role in our investigation, but we consider it an intriguing possibility worthy of future research.

It is also worth considering whether the attractive effects we have observed here are specific to faces. Our data do not rule out the possibility that a similar kind of integration across different features could also occur during the perception of complex objects or bodies. This latter idea is at least plausible; face- and body-selective regions occupy neighboring regions of temporal cortex (Weiner & Grill-Spector, 2013), macaque IT cells can respond to both bodies and heads (e.g., Ashbridge, Perrett, Oram, & Jellema, 2000; Perrett et al., 1992; Wachsmuth, Oram, & Perrett, 1994), and rotated bodies can influence the latency of eye gaze judgments (Seyama & Nagayama, 2005). In any case, emergent integration is, at the very least, particularly relevant for understanding how faces are processed and perceived, and our investigation makes a novel contribution by characterizing its operation across time.

Gaze discrimination orchestrates many important social behaviors, including joint attention (e.g., Driver et al., 1999), communication (Argyle & Cook, 1976), and inferring another person's state of mind (Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & Walker, 1995; Calder et al., 2002). Here we showed that just as these social processes occur across time, so too does the emergent perception of a person's direction of gaze. This integrative process appears to be constrained by temporal boundaries of object continuity, and yet at the same time, may provide stability in the way people perceive one another.

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