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The role of gaze direction in face viewpoint aftereffect

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Face viewpoint aftereffect is a visual illusion that, after adaptation to a face side view, the perceived view direction of the same face subsequently presented near its front view is biased in a direction opposite to that of the adapted view. Eye gaze is a unique component in face not only because its direction is relatively independent of face view direction, but also because it is a primary cue for conveying social attention. Here we studied the contribution of gaze direction adaptation to the formation of face viewpoint aftereffect. We found that a tiny (in terms of relative area) change of gaze direction in adapting face stimuli could induce a dramatic reduction in the magnitude of face viewpoint aftereffect. However, vertical inversion of the face stimuli almost abolished the reduction. Implications of these findings about face view representation and gaze direction representation are discussed.

1. Introduction

Visual adaptation has been dubbed the psychophysicist's microelectrode because the resulting visual aftereffects could be utilized to infer selective neural sensitivities to various stimulus dimensions, from low-level stimulus features (Anstis & Moulden, 1970; Blakemore & Campbell, 1969; Kohler & Wallach, 1944) to mid-level surface and shape properties (Regan & Hamstra, 1992; Suzuki & Grabowecky, 2002; van Lier, Vergeer, & Anstis, 2009), to high-level object and face properties (Fang & He, 2005; Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Watson & Clifford, 2003; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & Maclin, 1999; Zhao & Chubb, 2001). For example, adaptation to a leftward or rightward gaze/face view could bias our percept of gaze/face view direction opposite to the adapted direction. These illusions were termed gaze direction aftereffect (Jenkins, Beaver, & Calder, 2006) and face viewpoint aftereffect (Fang & He, 2005; Ryu & Chaudhuri, 2006), which suggest a multichannel system comprising separate channels for coding different gaze directions or face views (Calder, Jenkins, Cassel, & Clifford, 2008). These two aftereffects have also received attention beyond vision research areas because face and gaze directions are primary cues for conveying social attention and they have been the focus of a large body of 'social attention' studies in recent years (Nummenmaa & Calder, 2009).

Many single-unit recording and functional magnetic resonance imaging (fMRI) studies have been carried out to study neural representations of gaze direction and face view in monkey and human visual system. In monkey subjects, Perrett and colleagues (1991) found that the majority of neurons in the anterior superior temporal sulcus (STS) exhibited face view selectivity and most of them showed a unimodal tuning property, which has been confirmed by other groups (De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Desimone, Albright, Gross, & Bruce, 1984; Hasselmo, Rolls, Baylis, & Nalwa, 1989). Such neurons were also found in the inferior temporal cortex (IT) (Desimone et al., 1984). Although investigated less extensively, neurons tuned to distinct gaze directions were also identified in STS (Perrett, Hietanen, Oram, & Benson, 1992). And bilateral STS ablation could impair gaze perception specifically (Campbell, Heywood, Cowey, Regard, & Landies, 1990). In human subjects, using an fMRI adaptation paradigm, Fang, Murray, and He (2007) demonstrated that face views were represented in STS and FFA (fusiform face area) (see also Andrews & Ewbank, 2004). Hoffman and Haxby (2000) showed that attending to gaze direction could activate STS more strongly than attending to face identity, suggesting the important role of STS in gaze perception. An fMRI adaptation study by Calder and colleagues (2007) provided clear evidence for separate neuronal populations in STS coding left and right gaze.

In summary, converging evidence has identified STS as a critical area for coding both gaze direction and face view. A natural question to ask is how the neural representations of gaze direction and face view influence each other. The interaction of view direction and gaze direction might convey different cues to social attention and perhaps links to more general proposals regarding the role of STS in processing intentionality (Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009). Several human behavioral studies have shown an influence of view direction on the perception of gaze direction and vice versa (Langton, 2000; Langton, Honeyman, & Tessler,

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2004; Ricciardelli & Driver, 2008). De Souza and colleagues (2005) elaborately investigated the function of different parts of anterior STS in macaque monkeys and found that modulation of the responses of face view-selective neurons by gaze direction was evident in the rostral part of anterior STS (see also Perrett et al., 1992). Specifically, neuronal responses to a face side view could be either enhanced or inhibited by the gaze direction simulating eye contact directed toward subjects (a similar stimulus can be found in Fig. 1A in the incongruent condition), but the proportion of the enhanced neurons was significantly larger than that of the inhibited neurons.

In this study we took advantage of face view point aftereffect to investigate this issue. For a face image, its view direction and gaze direction are relatively independent. And both view direction adaptation and gaze direction adaptation might contribute to the formation of face view point aftereffect. To separate these two adaptation effects, in the first experiment we manipulated face view direction and gaze direction independently in our stimuli. The adapting stimulus was a face side view, but the gaze could be either consistent with the face view or projected toward the subject (i.e. simulating eye contact). By comparing the magnitudes of face view point aftereffect in these two conditions we examined how the gaze direction modulated the face view point aftereffect. In addition, to test if the modulation (if there was any) was simply due to the face image difference between these two conditions, we carried out the second experiment in which all the stimuli were vertically inverted. Since the image difference was the same in these two experiments, any difference in the modulation effect should be attributed to the specific role of gaze direction in face view point aftereffect.

Fig. 1. Face stimuli in Experiment 1 (A and B) and Experiment 2 (C and D). (A) Adapting stimuli are the 30° side views (left and right) of a face. Their gaze direction and face view direction are either congruent (left column) or incongruent (right column). (B) Test stimuli are the front view (0°) and 3°, 6° side views (left and right) of the face. Their gaze direction and face view direction are congruent. (C and D) Vertical inversions of the stimuli in (A) and (B).

2. Experiments 1 and 2

2.1. Methods

2.1.1. Participants

Six naive subjects (2 male and 4 female) with normal or corrected to normal vision participated in both Experiments 1 and 2. They gave written, informed consent in accordance with procedures and protocols approved by the human subject review committee of Peking University.

2.1.2. Apparatus and stimuli

Stimuli were presented on an IIYAMA color graphic monitor (model: MM906UT; refresh rate: 100 Hz; resolution: 1024 × 768; size: 19 in.). The viewing distance was 57 cm. In Experiment 1, the adapting and test stimuli were upright faces and they were generated by projecting a 3D face model with different in-depth rotation angles onto the monitor plane, with the front view as the initial position; 30° rotation for adaptors; and 0°, 3°, and 6° rotation for test stimuli. Both left and right rotations were executed. FaceGen Modeller 3.1 (http://www.facegen.com/) was used to generate the 3D face model and manipulate the gaze direction of the face. For the adaptors, the gaze direction could be either the same as the face view direction (congruent condition) or simulate eye contact directed toward the subject (incongruent condition) (Fig. 1A). For the test stimuli, the gaze direction was the same as the face view direction (Fig. 1B). In Experiment 2, the adapting and test stimuli were the vertical inversions of the stimuli in Experiment 1 (Fig. 1C and D). All the stimuli extended no more than 3.2° × 3.2°.

2.1.3. Experimental procedure

In Experiments 1 and 2, there were two adaptation conditions (gaze direction and face view direction were congruent or incongruent) and one baseline condition (no adaptation). Each adaptation condition had ten blocks (five blocks with the left side view adaptor and the other five with the right side view adaptor), and the baseline condition had five blocks. Each block consisted of 50 trials. In Experiment 1, for the two adaptation conditions, subjects adapted to the 30° side view of the face, and the five test stimuli were always the front view (0°) and 3° and 6° side views (left and right). Each adaptation block began with a 25 s pre-adaptation. After a 5 s topping-up adaptation and a 1 s blank interval, one of the five test stimuli was presented for 0.2 s and subjects were asked to make a two-alternative forced-choice (2-AFC) judgment of the view direction of the test stimulus, either left or right (Fig. 2). To avoid local adaptation during the adaptation period, the adapting stimulus floated randomly within a 5.7° × 5.7° area, whose center was coincident with the center of the monitor. The starting point of the adapting stimulus was also randomly distributed in this 5.7° × 5.7° area, and its floating velocity was 0.85°/s. The position of the test stimulus was randomly distributed within the 5.7° × 5.7° area too. During the experimental period, a fixation point was placed in the center of the monitor and subjects were required to maintain fixation. In all the adaptation blocks, each of the five test stimuli was presented 10 times, for a total of 50 stimulus presentations/trials with a random sequence. All of the data from the ten blocks were pooled together for analysis. The baseline condition was very similar to the adaptation conditions except that subjects were asked to judge the view direction of the test stimulus without any adaptation. The temporal order of a total of 25 (2 × 10 + 1 × 5) blocks was randomized across experimental conditions. Subjects were given one practice block for each experimental condition before the main experiment. In Experiment 2, the procedure was the same as that of Experiment 1, but the stimuli were the vertical inversions of those in Experiment 1.

For both Experiments 1 and 2, data were collected in 2–3 sessions. Experiment 1 was carried out before Experiment 2. However, we re-run Experiment 1 with three of the six subjects after Experiment 2. Their data showed a very similar pattern as before, which suggested that the experimental order was not a confound.

2.2. Results

The results are presented in Fig. 3 as psychometric functions: the percentage of trials in which subjects indicated that the view direction of the test faces was opposite to the adaptor plotted as a function of their true view direction. In both experiments without any adaptation, subjects gave nearly perfect performance for all five test stimuli (50% level for the front view, correct identification for the 3° and 6° test stimuli; see the black lines in Fig. 3). In other words, subjects had no trouble discriminating view directions of 3° and 6° from the front view. However, after adaptation to the 30° side view of the upright or inverted face, the psychometric functions showed a general horizontal shift to the left for both the congruent and incongruent conditions (compare the black lines with the dark gray and light gray lines in Fig. 3). The front views were often judged as facing away from the adapted view direction and even some of the test stimuli facing in the same direction as the adaptors were perceived as facing the direction opposite to that of the adaptors.

To quantitatively measure the magnitude of the view point aftereffect, psychometric values at the five test views were fit by using a cumulative normal function for individual subjects. We interpolated to find the view expected to be seen as the front view in 50% of the trials before and after adaptation. We quantified the magnitude of the view point aftereffect as the angular difference between the views found through interpolation before and after adaptation (i.e. a horizontal shift between the cumulative normal functions). In Experiment 1, the magnitudes were significantly above 0 for both the congruent condition (Mean ± SEM: 1.21 ± 0.23; $t(5) = 5.16$, $p = 0.004$) and the incongruent condition (Mean ± SEM: 0.77 ± 0.16°; $t(5) = 4.74$, $p = 0.005$). The magnitude for the congruent condition was significantly larger than that for the incongruent condition ($t(5) = 3.057$, $p = 0.028$) (left panel of Fig. 3). In Experiment 2, the magnitudes were also significantly above 0 for both the congruent condition (Mean ± SEM: 1.69 ± 0.36; $t(5) = 4.71$, $p = 0.005$) and the incongruent condition (Mean ± SEM: 1.52 ± 0.32; $t(5) = 4.77$, $p = 0.005$). But there was no significant difference between these two conditions ($t(5) = 1.068$, $p = 0.334$) (right panel of Fig. 3). We also compared the magnitudes for the congruent condition between Experiments 1 and 2ae

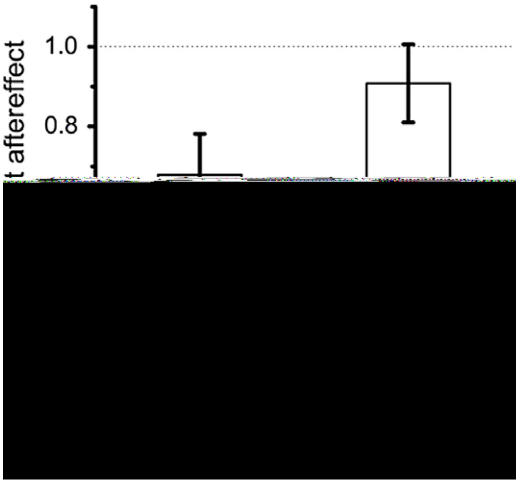

Fig. 4. Normalized viewpoint aftereffects for the incongruent adaptation condition in Experiment 1 (upright face) and Experiment 2 (inverted face). When the gaze direction and face view direction of the adapting stimulus are congruent, the magnitude of the viewpoint aftereffect was set to 1. Error bars denote 1 SEM.

3. Experiment 3

Experiment 1 demonstrated that face side views with incongruent gaze induced a significantly weaker viewpoint aftereffect than those with congruent gaze. One possible explanation is that the side views with incongruent gaze might be perceived as being closer to the front view than those with congruent gaze, thus they could be considered as weaker adaptors. In Experiment 3, we attempted to measure the effect of gaze direction on perceived face view direction.

3.1. Methods

3.1.1. Participants

Six naive subjects (4 male and 2 female) with normal or corrected to normal vision participated in Experiment 3. Three of them also participated in Experiments 1 and 2. They gave written, informed consent in accordance with procedures and protocols approved by the human subject review committee of Peking University.

3.1.2. Apparatus and stimuli

The apparatus and the face model were the same as those used in Experiments 1 and 2. The viewing distance was 57 cm. Sample faces were the adapting stimuli in Experiment 1, 30° side views. Their gaze direction and face view direction could be congruent or incongruent. Test faces were 24°, 27°, 30°, 33° and 36° side views. Their gaze direction and face view direction were congruent. All the stimuli extended no more than 3.2° × 3.2°.

3.1.3. Experimental procedure

Subjects were instructed to discriminate face view directions. In a trial, a sample face and a test face were each presented for 200 ms, separated by a 400 ms blank interval (Fig. 5A). The order of the sample face and the test face was randomized. Subjects needed to make a 2-AFC judgment of the direction of the second face relative to the first face (left or right). Each subject completed a total of 16 blocks, 8 blocks with left side views and the other 8 blocks with right side views. Each block contained 50 trials, 25 trials with the congruent sample face and the other 25 trials with the incongruent sample face. The five test faces were each presented 10 times, and were randomly distributed in a block. All of the data from the 16 blocks were pooled together for analysis.

The face stimuli were randomly presented within a 5.7° × 5.7° area, whose center was coincident with the center of the monitor. During the experimental period, a fixation point was placed in the center of the monitor and subjects were required to maintain fixation.

3.2. Results

The results are presented in Fig. 5B as psychometric functions: the percentage of trials in which subjects indicated that the view direction of the test faces was more tilted from the front view than the sample face plotted as a function of their view direction. It is apparent that, comparing to the congruent sample face, the incongruent sample face that simulated eye contact was judged to be closer to the front view.

To quantitatively measure the effect of gaze direction on perceived face view direction, psychometric values at the five test views were fit by using a cumulative normal function for individual subjects. We interpolated to find the view matching the perceived view direction of the congruent and incongruent sample faces. Mean view directions averaged across subjects were 29.9° and 28.4° for the congruent and incongruent sample faces, respectively. The effect was small (1.5°), but significant ($t(5) = 3.272$, $p = 0.022$).

4. Discussion

We observed a significant viewpoint aftereffect after adapting to an upright face or an inverted face, regardless of whether the face view direction was the same as the gaze direction or not. But the modulation effect of gaze direction was evident only for the upright face. These findings shed light on the neural representations of face view and gaze direction and their interaction.

Although both face view adaptation and gaze adaptation might contribute to the formation of face viewpoint aftereffect, it was unclear to what extent gaze adaptation could contribute to the aftereffect, especially considering that the gaze occupies a very small portion of the face (i.e. 1.7% in our stimuli). Surprisingly, keeping the gaze directed toward subjects in the adapting face resulted in about 1/3 reduction of the magnitude of the viewpoint aftereffect. In other words, the transfer of viewpoint aftereffect between faces with different view-gaze configurations was only 68%. In a previous study, using the same experimental procedure, Fang, Ijichi, and He (2007) found that the transfer of viewpoint aftereffect between faces with different identities was 82%. This comparison demonstrates the special and important role of gaze direction in face viewpoint aftereffect – a tiny gaze change (in terms of relative area) has a more profound effect than a whole face identity change!

The results in Experiments 2 and 3 rule out two potential explanations of the gaze modulation effect in Experiment 1 (upright face). One explanation is that the modulation effect was due to the face image difference between the adaptors in the congruent and incongruent conditions. However, the null effect in Experiment 2 renders this explanation impossible since the image difference was the same in Experiments 1 and 2. The other explanation is that the side views with incongruent gaze might be perceived as being closer to the front view than those with congruent gaze, thus they could be considered as weaker adaptors. In Experiment 3, we found that the direct gaze (i.e. looking at the subject) could bias the perceived direction of the adapting face view towards the front view by about 1.5°, which meant that the perceived direction of the adapting face view was about 28.5°. Recently, we measured the angular tuning function of the face viewpoint aftereffect, that is, how does the magnitude of the aftereffect depend on the angle between adaptor and test (manuscript in preparation). We found

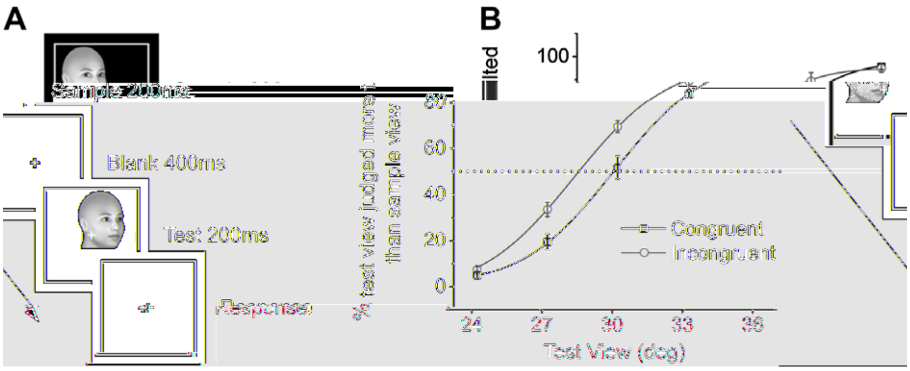

Fig. 5. Procedure and results in Experiment 3. (A) Schematic description of the experimental procedure. A sample face and a test face were presented successively. Subjects needed to make a 2-AFC judgment of the view direction of the second face relative to the first face (left or right). (B) Psychometric functions showing view direction judgments for the congruent and incongruent sample faces. Data points averaged across subjects were fit using a cumulative normal function. The abscissa refers to the view direction of the five test faces. The ordinate refers to the percentage of trials in which subjects indicated that the view direction of the test faces was more tilted from the front view than the sample face. Error bars denote 1 SEM.

that, as the angle increased from 0° to 90°, the aftereffect magnitude increased quickly, peaked at 20°, and then gradually decreased. These data suggested that the perceived change of face view direction should enhance (rather than attenuate) the aftereffect, which is opposite to the prediction from the second explanation.

Our psychophysical data, along with previous electrophysiological and neuroimaging studies, point to the determinative role of neural circuits in STS in the face viewpoint aftereffect. First, in the study by Fang et al. (2007), we speculated that the strong transfer of the face viewpoint aftereffect between faces with different identities is due to the fact that view-selective face neurons in STS are generally not sensitive to identity (Perrett et al., 1992). Second, the significant reduction of face viewpoint aftereffect by the incongruent gaze direction can be explained by the existent findings in STS. One explanation is that both face view and gaze direction are coded in STS and their neural representations contribute to the formation of the viewpoint aftereffect (Andrews & Ewbank, 2004; Calder et al., 2007; Fang et al., 2007). However, only face view adaptation took effect in the incongruent condition. A second explanation is that neuronal responses to a face side view could be modulated (either enhanced or inhibited) by the direction simulating eye contact directed towards subjects, and the net modulation effect at population level was enhancement (De Souza et al., 2005) which might counteract the adaptation effect and lead to a weaker aftereffect. It should be noted that these two explanations are not mutually exclusive.

Why does the incongruent gaze direction have little effect with the inverted face image? Although vertical inversion does not affect subjects' percept of face view direction (Fig. 3, baseline condition), it has been shown that sensitivity for gaze direction could be severely impaired by such an inversion (Jenkins & Langton, 2003; Schwaninger, Lobmaier, & Fischer, 2005). Decreased sensitivity might lead to less gaze direction-specific adaptation and less modulation of the viewpoint aftereffect consequently (Clifford & Rhodes, 2005; Murray & Wojciulik, 2004).

In summary, using psychophysical adaptation, we demonstrated the important role of gaze direction in modulating the magnitude of viewpoint aftereffect, suggesting a close relationship between face view representation and gaze direction representation. We also showed that vertical inversion of face images could abolish the modulation effect. Studying the representations of face view and gaze direction not only advances our understanding of the neural mechanism of face perception, but also help to understand how humans possess remarkable social attention skills since social attention is conveyed primarily by gaze direction and face view direction. Almost all previous researches studied gaze and face view separately (Nummenmaa & Calder, 2009). In future research, more psychophysical, brain imaging and single-unit studies are needed to carry out to obtain a full understanding of the interaction between gaze direction and face view and its biological significance.

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