A real head turner: Horizontal and vertical head directions are multichannel coded

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Head direction is a salient cue to the focus of other people’s attention. Electrophysiology in macaques has shown head-selective cells in the superior temporal sulcus that are mostly tuned to different directions (up, down, left, right, front, back, etc.). However, there has been no systematic investigation into the visual representation of head direction in both the horizontal (left–right) and vertical (up–down) planes in humans. We addressed whether the coding of head direction is best accounted for by a multichannel system, with distinct pools of cells (or channels) tuned to different head views (i.e., left, right, direct, up, and down), or an opponent-coding system with two broadly tuned pools of cells responding to two extremes (i.e., left–right and up–down) and “direct” represented as the equilibrium state in the system. In a series of four experiments, we carried out two adaptation procedures for which multichannel and opponent coding predict distinct outcomes. The results support multichannel coding of head direction in both the vertical and horizontal axes.

Keywords: adaptation, head direction, multichannel coding, opponent coding, aftereffects


Introduction

The mechanisms underlying social attention have been the focus of a large body of recent research (Nummenmaa & Calder, 2009); for both humans and non-human primates successful social interaction depends on the ability to judge accurately where others are attending. Humans readily use head direction as a cue to gauge where other people are attending, especially when information from eye gaze is obscured or insufficient. Among other movements, the human head can be rotated from left to right and flexed/extended from up to down signaling attention in both the horizontal and vertical axes. Seminal electrophysiological studies in macaques identified cells sensitive to head direction in the anterior superior temporal sulcus (STS). These head-selective cells were broadly tuned with the majority coding prototypical views such as left profile, right profile, direct, up, and down (Perrett et al., 1985). A small number of cells found were tuned to individual identities and were thought to be implicated in coding view-specific representations of facial identity. Many cells, however, were invariant to identity and it was proposed that these may have a role in the perception of others’ direction of attention (Perrett et al., 1991).

Recent psychophysical studies in humans have demonstrated view-specific coding of faces in what the authors have termed the “viewpoint aftereffect” (Fang & He, 2005). In this study, faces were one type of stimulus used to test for object-selective neurons tuned to specific viewpoints in the human brain. The results showed that after adapting to a face oriented 30° to the left (or right), an aftereffect occurs in which front-facing presentations of the same face appear oriented opposite to the adapted direction. Such effects have since been shown to persist across changes in the gender and identity of the adaptation and test faces (Fang, Ijichi, & He, 2007). Fang and He (2005) also demonstrate a reduced magnitude of adaptation as a function of the angular difference between adaptor and test stimuli, such that 60° adaptor heads produced significantly smaller aftereffects than 30° adaptors. The authors included the 60° adaptors as a means of demonstrating that their effects could not be due to motion-related artifacts. However, this finding is also consistent with a representational system comprising multiple distinct neural populations (or channels) sensitive to specific viewpoints. In such a system, at least where each neural population is narrowly tuned to a range of head directions, 60° adaptor stimuli will have less of an effect than 30° adaptors on the firing rate of cells coding the test stimulus and hence produce smaller aftereffects. However, whether this type of system provides the optimal account of representing head orientation has not been systematically tested. In addition, it is important to note that the stimuli used in Fang et al.’s experiments depicted oriented heads with the eyes open. Given that
adaptation to left and right eye gaze has been shown to produce direction-specific eye gaze aftereffects (Calder et al., 2007; Jenkins, Beaver, & Calder, 2006), it is conceivable that aftereffects reported by Fang and He may be partly driven by the eyes. Thus, less adaptation might be found when the adaptor head angle is 60° because information from the eyes is partially obscured. These head direction adaptation studies generally support a functional dissociation between the coding of left and right head directions in humans. However, this is compatible with either of two representational systems: opponent coding, based on two broadly tuned opponent channels (or cell populations), each of which responding maximally to stimuli at one extreme of a central tendency, or norm, or multichannel coding, with distinct channels (or cell populations) tuned to different stimulus dimensions. Hence, the sensory coding underlying the visual representation of horizontal head direction in humans remains unclear.

Multichannel coding has been applied to account for the representation of directional cues, such as line orientation, and socially salient cues, such as gaze (Calder, Jenkins, Cassel, & Clifford, 2008; Clifford, 2002; Suzuki, Clifford, & Rhodes, 2005). The simplest conceivable multichannel model of horizontal head directions ranging from left profile, through direct, to right profile would comprise separate channels (or cell populations) for the three distinct orientations (left, direct, right; Figure 1a). Of course, more than three channels would be necessary to represent all possible horizontal head views, including back views. In contrast, opponent coding has been shown to account for the representation of perceptual dimensions that behave in an antagonistic fashion, such as color (e.g., red–green; Webster, 1996) and aspect ratio (Regan & Hamstra, 1992). Furthermore, recent investigations into “high-level” configural face processing have been taken as evidence of opponent coding in the representation of facial identity (Leopold, O’Toole, Vetter, & Blanz, 2001; Rhodes & Jeffery, 2006; Robbins, McKone, & Edwards, 2007), whereby individual facial dimensions constitute separate opponent-coded mechanisms. An opponent-coding model of horizontal head directions would comprise one channel

Figure 1. Opponent versus multichannel coding. The graphs on the left schematically represent the responses of a multichannel system with three hypothetical channels preferring heads oriented to the left (or down in the case of vertical head direction; red), heads facing directly ahead (black), and heads oriented to the right (or up in the case of vertical head direction; blue). The graphs on the right schematically represent the responses of an opponent-coding system comprising two hypothetical opponent-coded pools of cells preferring heads oriented to the left (or down in the case of vertical head direction; red) and heads oriented to the right (or up in the case of vertical head direction; blue). The graphs show responses in the baseline condition (a, d), following adaptation to alternating left–right (or up–down) oriented heads (b, e), and following adaptation to direct-facing heads (c, f). Gray-shaded regions indicate the range in which a probe would be categorized as “direct” and is determined by the crossover points between the channels. In the graphs for adaptation conditions, dashed lines represent engagement following adaptation; for purposes of comparison, responses in the baseline condition are graphed as solid lines. The bar graphs at the top of the figure indicate the proposed engagement of each channel for three optimal stimuli: left- (or down), direct-, and right- (or up) oriented heads.
maximally responsive to left orientations and another maximally responsive to right orientations, with ‘direct’ represented as the equal engagement of left and right channels (Figure 1d).

The human head is not limited to signaling attention to the left and the right, and it can also be flexed and extended to signal attention both up and down. While a number of studies have investigated the factors involved in the perception (Langton, 2000; Wilson, Wilkinson, Lin, & Castillo, 2000) and neural representation (Fang & He, 2005; Fang, Ijichi et al., 2007; Fang, Murray, Kersten, & He, 2005) of horizontal head direction, surprisingly little research has investigated vertical head direction perception in humans. However, single-cell recording studies in macaques have identified cells that are sensitive to the orientation of the head in the vertical axis but are relatively unaffected by heads in the horizontal axis (Perrett, Hietanen, Oram, & Benson, 1992; Perrett et al., 1991, 1985). A number of cells that were maximally sensitive to heads rotated upward (but unresponsive to full face, profile, or heads rotated down) were identified, whereas a distinct population of cells showed the opposite response profile (i.e., they were more responsive to heads oriented downward than to full face or upward-oriented heads). Similarly, we hypothesize that up and down head orientations are represented as separate channels (or neuronal populations) in humans; however, this hypothesis is also compatible with either multichannel or opponent coding.

The present study sought to address whether identity-invariant, view-specific cells representing different head directions exist in humans and if so, which perceptual framework best accounts for the visual representation of these cues to social attention. We used adaptation to address the perceptual basis of head direction in the horizontal (Experiments 1 and 2) and vertical (Experiments 3 and 4) axes. Specifically, we aimed to determine whether head direction is represented by an opponent-coded or multichannel system. To distinguish between these accounts, we used two adaptation paradigms for which multichannel- and opponent-coding models predict distinct outcomes (Calder et al., 2008), and in doing so, we assume that the following two principles apply to these models. First, head direction is calculated by considering the output of all channels, the balance of both left and right channels for opponent coding of horizontal orientations, or the weighted sum of all channels for a multichannel system. Second, adaptation reduces any subsequent response of a channel in proportion to its sensitivity to the adapting stimulus.

To distinguish between multichannel and opponent coding of head orientation, in Experiment 1 participants adapted to an alternating sequence of heads oriented 20° left and 20° right, whereas in Experiment 2 participants adapted to direct (0°) oriented heads. In a multichannel model, adapting to alternating left- and right-oriented heads would attenuate the left and right channels equally and the direct channel to a lesser extent. The difference in responsiveness between the three channels would result in an increased tendency to categorize left- and right-oriented heads as “direct” (Figure 1b). In contrast, adaptation to direct-facing heads would attenuate the direct channel more than the left and right channels resulting in a decreased tendency to categorize left- and right-oriented heads as “direct” (Figure 1c). Thus, a multichannel model predicts opposite effects on the range of head directions classified as “direct” following adaptation to alternating left–right heads (Experiment 1) versus direct-facing heads (Experiment 2).

If head direction were opponent-coded, then adapting to alternating left- and right-oriented heads would result in equal attenuation of both left and right channels (Figure 1e). Adaptation to direct-facing heads would also predict equal attenuation of these channels, although to a lesser extent than alternating left–right adaptation (Figure 1f). In neither case would there be a change in the crossover point between channels. Hence, it is possible that neither would result in a change in head orientation discrimination. However, in deriving the predictions of opponent coding, it is important to consider the issue of just how equal the responses of these channels need to be in order for a head orientation to be classed as “direct.” If, for example, a proportional decision rule was assumed and the ratio of the left and right channel responses needed to be between certain limits (around a value of 1) for a head direction to be classed as “direct,” then it is conceivable that equal adaptation of both channels could change the range of head directions producing this response ratio and, hence, increasing the range classified as “direct,” without changing the crossover point between channels.

However, for our present study, the critical factor is that opponent coding predicts that two channels are adapted equally for both the alternating left–right (Experiment 1) and direct adaptation (Experiment 2), the only difference being the overall magnitude of the adaptation. Thus, there is no way for an opponent-coding system to accommodate the predictions of a multichannel model, that is, opposite effects on the range of head directions classified as “direct” following adaptation to alternating left–right heads (Experiment 1) versus direct-facing heads (Experiment 2).

Experiments 3 and 4 sought to distinguish between multichannel and opponent coding of heads in the vertical (up–down) axis and provide the first demonstration of adaptation to vertical head directions in humans. Here, we assume that multichannel and opponent coding of vertical head orientation operate in the same manner to the horizontal axis. Hence, the predictions of the two models for head orientation in the vertical axis are essentially the same as those for the horizontal axis. In other words, the multichannel model predicts that adapting to alternating presentations of up- and down-oriented heads should
produce an opposite effect to adapting to direct-facing heads. By contrast, the opponent-coding model is unable to accommodate opposite effects for these two conditions.

**Experiment 1—“Alternating left–right” adaptation**

**Methods**

**Participants**

Sixteen right-handed volunteers (10 females; mean age 21.3 years ($SD = 1.61$); range 20–25 years) took part in this experiment. Participants in this and all following experiments were recruited from the MRC Cognition and Brain Sciences Unit Volunteer panel and were paid for participating. All had normal or corrected-to-normal vision.

**Materials**

Grayscale images of computer-generated heads with their eyes closed were used as probes and adaptation stimuli. Images were created using DAZ 3D software (http://www.daz3d.com/) and depicted 10 different identities (5 males, 5 females). For the probes, each identity showed 5 different angles of head orientation: 8° left, 4° left, 0° direct, 4° right, and 8° right (50 images in total). Adaptation stimuli consisted of the same 10 identities with heads oriented 20° to the left and right. Sample stimuli are shown in Figure 2a. Probe stimuli measured 3 cm vertically and 2.5 cm horizontally, subtending a visual angle of approximately $3° \times 2.5°$ at a viewing distance of 57 cm. Adaptation stimuli were 25% bigger than probe stimuli to disrupt low-level retinotopic mapping between the two. A headrest was used throughout to ensure a constant viewing distance and head position. Crucially, adaptor and probe head images had their eyes closed; therefore, any aftereffects observed arise from directional information signaled by the head alone.

**Design and procedure**

All of the reported experiments, including Experiment 1, comprised three phases: a first baseline phase, an adaptation phase, and a second baseline phase (Figure 2b). The first baseline phase occurred prior to any adaptation and provided practice in categorizing the probe head orientations and a measure of participants’ ability to discriminate different probe head directions. This was repeated at the end of the experiment as a post-adaptation baseline phase. The adaptation phase comprised two sections: Section 1, in which participants adapted to an alternating sequence of 20° left- and 20° right-oriented heads and a top-up section (Section 2) in which participants were retested with the same probe head images from the baseline blocks, but each probe was preceded by a top-up adaptation sequence as outlined below.

**Baseline phases**

The baseline phases comprised two identical pre-adaptation baseline blocks (baselines 1 and 2: Figure 2b(i) and two further identical blocks (baselines 3 and 4: Figure 2b(iii)) presented post-adaptation. In each block, 10 identities were shown in 5 orientations: 8° left, 4° left, 0°, 4° right, and 8° right (50 stimuli in total). Trials consisted of a probe head for 200 ms and then a 1800-ms ITI. Presentation order was randomized and participants categorized each head direction as “left,” “direct,” or “right.” Participants had 1800 ms for response logging. Baseline 1 was used to familiarize participants with the task and was disregarded as practice. Baseline 3 was removed to eliminate any residual adaptation effects, as these have been shown to persist up to 385 s in adaptation studies on eye gaze (Kloth & Schweinberger, 2008). This left baselines 2 and 4 as measures of pre- and post-adaptation baseline performance respectively.

**Adaptation phase**

The adaptation phase contained two sections (Figure 2b(ii)). Section 1 consisted of an alternating sequence of 20° left- and 20° right-oriented heads. For each identity, the left- and right-directed exemplars were presented three times (60 stimuli in total). Each image was presented for 4000 ms followed by a 200-ms ISI to eliminate any “apparent” motion. Adjacent faces never showed the same identity. Participants were instructed to look at each image and make a gender judgment to ensure attention throughout.

Section 2 (the top-up section) contained the same probe heads as in the baseline blocks; however, each probe face was preceded by six top-up adaptor images, posed by two identities (one male, one female). Top-up images were presented in an alternating sequence of 20° left and 20° right. Each was presented for 1000 ms and separated from the next by a 200-ms ISI. On half of the trials, the top-up sequence ended with a 20° left head and on the other half with a 20° right head. This was followed by a 200-ms blank ISI and a 200-ms presentation of a probe face (clearly marked “respond”) and then a 1800-ms ITI for response logging. Again, participants were required to categorize the head direction of the probe image as “left,” “direct,” or “right.” To disrupt low-level retinotopic mapping, the top-up adaptor faces were a different identity to the probe faces and 25% bigger; hence, any adaptation effects are unlikely to reflect low-level aftereffects or adaptation of facial identity.
Results

A full summary of left, direct, and right responses to the probe heads at each phase in the experiment is shown in Table 1. As left- and right-oriented heads were never, or rarely, categorized as right or left, respectively (average <0.1%), data are summarized as mean percentage of “direct” responses to the probe heads and adaptation was measured as the change in “direct” responses between adaptation and baseline phases. Greenhouse–Geisser correction was used when appropriate in all the analyses of variance (ANOVA) reported, and t-test comparisons were Bonferroni-corrected ($p < 0.01$ corrected for 5 comparisons) with uncorrected $p$-values reported throughout. Prior to analysis, data were arcsine-transformed to stabilize variance of the proportion measures, which showed a range of values including values close to ceiling and floor. The patterns of results were identical to those

Figure 2. Trial format, sample stimuli, and procedure used throughout all experiments. Orientations of adaptor and probe stimuli (a) varied across experiments as shown. Ten different identities (exemplars of only a few shown) were used throughout. All experiments had a three-phase format (b) comprising (i) a first baseline phase (baselines 1 and 2), (ii) an adaptation phase, and (iii) a second baseline phase (baselines 3 and 4) identical to the first. The adaptation phase consisted of two sections. See the text for details of the procedures.
### Experiment 1

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<th></th>
<th>L8</th>
<th>L4</th>
<th>D0</th>
<th>R4</th>
<th>R8</th>
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<td><strong>Left responses</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Baseline 2</td>
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<td>0.82</td>
<td>0.03</td>
<td>0.01</td>
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<tr>
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<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Baseline 4</td>
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<td>0.06</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Average baseline</td>
<td>0.99</td>
<td>0.82</td>
<td>0.04</td>
<td>0.00</td>
<td>0.00</td>
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</table>

| **Direct responses** |    |    |    |    |    |
| Baseline 2          | 0.01 | 0.18 | 0.92 | 0.27 | 0.04 |
| Adapt left–right    | 0.09 | 0.45 | 0.99 | 0.63 | 0.11 |
| Baseline 4          | 0.00 | 0.17 | 0.91 | 0.27 | 0.03 |
| Average baseline    | 0.01 | 0.18 | 0.92 | 0.27 | 0.04 |

| **Right responses** |    |    |    |    |    |
| Baseline 2          | 0.00 | 0.00 | 0.05 | 0.72 | 0.95 |
| Adapt left–right    | 0.01 | 0.00 | 0.00 | 0.37 | 0.89 |
| Baseline 4          | 0.01 | 0.00 | 0.03 | 0.73 | 0.97 |
| Average baseline    | 0.00 | 0.00 | 0.04 | 0.72 | 0.96 |

Table 1. Mean proportion of left, direct, and right responses to the five probe head directions in Experiments 1 and 2. “Adapt left–right” (Experiment 1) and “Adapt direct” (Experiment 2) refer to data from the top-up section of these experiments. Head orientations are labeled as follows: Experiment 1: L8 = left 8°, L4 = left 4°, D0 = direct 0°, R4 = right 4°, and R8 = right 8°. Experiment 2: L6 = left 6°, L3 = left 3°, D0 = direct 0°, R3 = right 3°, and R6 = right 6°.

### Experiment 2

<table>
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<tr>
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<th>L6</th>
<th>L3</th>
<th>D0</th>
<th>R3</th>
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<td></td>
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<tr>
<td>Baseline 2</td>
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<td>0.59</td>
<td>0.03</td>
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<td>Adapt direct</td>
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<td>0.90</td>
<td>0.06</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>Baseline 4</td>
<td>0.98</td>
<td>0.72</td>
<td>0.02</td>
<td>0.00</td>
<td>0.01</td>
</tr>
<tr>
<td>Average baseline</td>
<td>0.98</td>
<td>0.65</td>
<td>0.03</td>
<td>0.00</td>
<td>0.01</td>
</tr>
</tbody>
</table>

| **Direct responses** |    |    |    |    |    |
| Baseline 2          | 0.01 | 0.41 | 0.91 | 0.41 | 0.05 |
| Adapt direct        | 0.00 | 0.10 | 0.91 | 0.11 | 0.00 |
| Baseline 4          | 0.01 | 0.28 | 0.95 | 0.39 | 0.02 |
| Average baseline    | 0.02 | 0.35 | 0.93 | 0.40 | 0.03 |

| **Right responses** |    |    |    |    |    |
| Baseline 2          | 0.00 | 0.00 | 0.06 | 0.58 | 0.94 |
| Adapt direct        | 0.00 | 0.00 | 0.03 | 0.88 | 1.00 |
| Baseline 4          | 0.01 | 0.00 | 0.03 | 0.61 | 0.97 |
| Average baseline    | 0.00 | 0.00 | 0.04 | 0.60 | 0.96 |

found using non-transformed data, and all principal effects were also found using non-parametric Wilcoxon signed-rank tests corrected for multiple comparisons.

Baseline 1 was disregarded as practice and Baseline 3 was removed to eliminate any residual adaptation effects. This left baselines 2 and 4 (Figure 3a), which were submitted to a repeated measures ANOVA investigating baseline (2 and 4) and head direction (8° left, 4° left, 0° direct, 4° right, and 8° right). Results showed a significant effect of head direction, \( F(2.0, 29.89) = 116.82, \) MSE = 507.46, \( \eta^2_p = 0.89, p < 0.001 \), reflecting more accurate categorization of direct and 8° head directions than 4° head directions. There was no main effect of baseline or interaction between baseline and head direction (\( F < 1 \)), demonstrating that baseline performance did not change significantly across the experiment (i.e., between the two baseline phases), and consequently, all remaining analyses compare adaptation to the average of baselines 2 and 4.

Relative to baseline, adaptation produced an increase in “direct” responses to 4° left-, direct-, and 4° right-facing heads (L4° t(15) = 4.45, direct t(15) = 3.83, and R4° t(15) = 6.14, \( p < 0.01 \)). There was a borderline increase in “direct” responses to 8° left heads that did not survive Bonferroni correction, \( t(15) = 2.51, p = 0.02 \), and no significant effect for 8° right, \( p > 0.1 \). These results reflect an increased tendency to categorize 4° left and 4° right head directions as “direct” and a corresponding increased tendency to categorize direct-facing heads as “direct” following alternating left–right adaptation.

The top-up adaptation sequence ended with a head oriented 20° to the left or 20° right on equal numbers of trials. It was therefore important to exclude the possibility that the observed adaptation was driven by the last image in the top-up sequence, such that the symmetric adaptation effects observed resulted from pooling over trials that ended with 20° left and 20° right adaptors. To investigate this possibility, we split the data into “end-left” and “end-right” trials and compared the proportion of “direct” responses in a two-way repeated measures ANOVA investigating final top-up image (end-left adapt and end-right adapt) and head direction. Figure 3c summarizes participants’ performance on end-left and end-right trials. As expected, the results showed a significant main effect of head direction, \( F(4, 60) = 95.17, MSE = 377.67, \eta^2_p = 0.86, p < 0.001 \). However, there was no main effect of final top-up image, \( F < 1 \), and crucially no interaction between final
Figure 3. Results of Experiments 1 and 2. For Experiment 1, the graphs show the mean percentage of “direct” responses to probes at each of the head orientations (a) in baselines 2 and 4 separately and (b) following adaptation to alternating heads oriented 20° to the left and heads oriented 20° to the right (average performance in baselines 2 and 4 is also shown) and for (c) adaptation top-up trials that ended with a left-facing adaptor and adaptation top-up trials that ended with a right-facing adaptor (average performance in baselines 2 and 4 is also shown). For Experiment 2, the graphs show the mean percentage of “direct” responses to probes at each of the heads orientations (d) in baselines 2 and 4 separately and (e) following adaptation to direct-facing heads (average performance in baselines 2 and 4 is also shown). Head orientations are labeled as follows: Experiment 1: L8 = left 8°, L4 = left 4°, D0 = direct 0°, R4 = right 4°, and R8 = right 8°. Experiment 2: L6 = left 6°, L3 = left 3°, D0 = direct 0°, R3 = right 3°, and R6 = right 6°. Error bars represent standard errors.
top-up image and head direction, $F = 1.5, p > 0.2$. Hence, adaptation was not driven by the final top-up image alone.

In summary, the results of Experiment 1 show that adaptation to an alternating sequence of 20° left- and 20° right-oriented heads produced an increased tendency to categorize small angles of left- and right-oriented heads as “direct” relative to baseline performance. Additional analyses demonstrated that these aftereffects were not “direct” relative to baseline performance. Additional analyses demonstrated that these aftereffects were not driven by the direction of the final top-up image alone.

### Experiment 2—“Direct” adaptation

#### Methods

**Participants**

Sixteen right-handed volunteers (10 females; mean age 24.4 years ($SD = 3.93$); range 20–33 years) participated in this experiment. None had taken part in Experiment 1.

**Materials**

The stimuli were created using the same software as Experiment 1 and portrayed the same 10 identities. In Experiment 1, participants showed very good baseline categorization of 4° left- and 4° right-oriented heads (average of only 18% direct responses for 4° left and 28% direct responses for 4° right). To ensure adequate scope to show a decreased tendency to categorize small head angles as “direct,” the task in Experiment 2 was made slightly harder. Therefore, each identity showed slightly lesser angles of head orientation than used in Experiment 1; 6° left, 3° left, 0° direct, 3° right, and 6° right (50 images in total). However, this did not affect the predictions in any way. Adaptation stimuli comprised the same ten identities with direct-oriented heads (i.e., 0°). The image sizes and visual angles of the adaptation and probe stimuli were identical to Experiment 1.

**Design and procedure**

Experiment 2 comprised three phases: a pre-adaptation baseline phase (baselines 1 and 2) that was repeated post-adaptation (baselines 3 and 4) and an adaptation phase that comprised two sections. The format of events in each trial was the same as Experiment 1 and can be seen in Figure 2b. The only exception was that the adaptor images comprised direct (0°)-facing heads (rather than alternating left- and right-oriented heads).

**Baseline phases**

Baseline blocks (1, 2, 3, and 4) were identical to Experiment 1 with the exception that the probe stimuli portrayed lesser angles of orientation: 6° left, 3° left, 0° direct, 3° right, and 6° right; 50 stimuli in total (Figure 2b).

#### Adaptation phase

The adaptation phase contained two sections as in Experiment 1 (Figure 2b). Section 1 comprised a series of direct (0°)-facing adaptor heads. Trial timings and format were identical to Experiment 1 in every other respect.

Section 2 was also identical to Experiment 1 except that the “top-up” adaptor faces comprised a series of six direct (0°) head images posed by two identities (one male, one female), which varied from trial to trial.

#### Results

Data are again summarized as participants’ mean percentage of direct responses. A full summary of left, direct, and right responses is shown in Table 1.

Once again, baseline 1 was disregarded as practice and baseline 3 was removed to eliminate any residual adaptation effects. Participants’ performance in baselines 2 and 4 (Figure 3d) were compared with a two-factor repeated measures ANOVA examining the effects of baseline (2 and 4) and head direction (6° left, 3° left, 0°, 3° right, 6° right). Results showed a significant main effect of head direction, $F(4,60) = 124.89, MSE = 250.74, \eta_p^2 = 0.89, p < 0.001$, reflecting more accurate categorization of direct and 6° head directions than 3° head directions. There was no main effect of baseline, $F < 1$, or interaction with this factor, $F = 2.24, p > 0.1$. Consequently, the remaining analyses compare adaptation to the average of baselines 2 and 4.

Following adaptation to direct-facing heads, participants showed a decreased tendency to categorize 3° left and 3° right head directions as “direct” in the top-up section of the adaptation phase; this is summarized in Figure 3e. A repeated measures ANOVA comparing adaptation (baseline, direct adapt) with head direction showed a significant main effect of adaptation, $F(1,15) = 52.11, MSE = 103.02, \eta_p^2 = 0.78, p < 0.001$, reflecting a decrease in the number of “direct” responses made following adaptation relative to baseline. As expected, there was also a main effect of head direction, $F(2,61, 39.18) = 171.87, MSE = 268.70, \eta_p^2 = 0.92, p < 0.001$, and these main effects were qualified by a significant adaptation × head direction interaction, $F(4,60) = 15.51, MSE = 60.30, \eta_p^2 = 0.51, p < 0.001$.

Paired $t$-tests comparing each orientation in the baseline and top-up phases showed a decreased tendency to categorize 3° left- and 3° right-facing heads as “direct” following adaptation, $L3^\circ \tau(15) = 4.67, R3^\circ \tau(15) = 5.87, ps < 0.001$. There were no significant effects for 6° left or 6° right, $ps > 0.04$, or direct, $p > 0.4$. To ascertain whether the reduction in “direct” responses to the 3° left and 3°
right probes reflected an increase in “left” and “right” responses, respectively, we compared the proportion of “right” and “left” responses to probes following adaptation relative to baseline. Results showed that direct adaptation produced a significant increase in “right” responses to 3° right probes, \( t(15) = 5.97, p < 0.001 \), and similar increase in “left” responses to 3° left probes, \( t(15) = 4.87, p < 0.001 \).

Experiments 1 and 2—Discussion

Adaptation to an alternating sequence of 20° left- and 20° right-oriented heads (Experiment 1) produced an increased tendency to categorize small angles of left- and right-oriented heads as “direct” relative to baseline performance. Furthermore, it has been demonstrated that the effects are not driven by the direction of the final top-up image in the sequence of top-up adaptors and therefore reflect simultaneous adaptation of neural populations representing left and right head directions. In contrast, adaptation to direct (0°)-facing heads (Experiment 2) produced a decreased tendency to categorize small angles of left- and right-oriented heads as “direct” relative to baseline. This has been shown to reflect an increased tendency to correctly categorize these head directions as “left” and “right,” respectively. These opposite effects of adaptation are predicted by a multichannel-coding model. An opponent-coding model could not accommodate such opposite findings, and therefore, consistent with recent research on eye gaze and body direction adaptation (Calder et al., 2008; Jenkins et al., 2006; Lawson, Clifford, & Calder, 2009), these results support multichannel coding of head direction in the horizontal plane.

Perrett et al.’s (1985) single-cell investigations of macaque STS neurons identified cells that were maximally sensitive to up- and down-oriented heads in addition to those selective for horizontal head directions. Experiments 3 and 4 therefore use the same sort of adaptation paradigms as Experiments 1 and 2 to provide the first evidence of comparable representations of up- and down-oriented heads in humans and to determine whether the perceptual representation of head direction in the vertical axis is best accounted for by multichannel or opponent coding.

Experiment 3—“Alternating up–down adaptation”

Materials

The probe stimuli for this experiment were created using the same software as the previous two experiments and portrayed the same 10 head identities (5 males and 5 females). Each identity showed 5 different angles of head orientation in the vertical plane: up 10°, up 6°, direct 0°, down 6°, and down 10° (50 images in total; see Figure 2a). Pilot testing showed that 6° and 10° were optimal to provide baseline performance that was able to show either increases or decreases in “direct” responses (i.e., around 50% “direct” responses to 6° angles of head orientation). Adaptation stimuli depicted each of the ten identities with heads oriented 20° up and 20° down. Adaptation and probe stimuli were the same size as those used in Experiments 1 and 2.

Design and procedure

Experiment 3 had the same three-phase format as Experiments 1 and 2, comprising a pre-adaptation baseline phase (baselines 1 and 2), followed by a two-section adaptation phase and a post-adaptation baseline phase identical to the first (baselines 3 and 4; see Figure 2b).

Baseline phases

Trials within the baseline blocks (1, 2, 3, and 4) had an identical format to Experiments 1 and 2 with the exception that the probe stimuli portrayed heads oriented in the vertical plane and participants categorized them as “up,” “direct,” or “down.”

Adaptation phase

The adaptation phase contained two sections (Figure 2b). Section 1 used an identical presentation format to Experiment 1 and consisted of an alternating sequence of 20° up- and 20° down-oriented heads. Section 2 contained the same probe heads as in the baseline blocks which participants categorized as “up,” “direct,” and “down.” Like the previous experiments, each probe face was preceded by six top-up adaptor images that were posed by two identities (one male, one female) and presented in an alternating sequence of 20° up and 20° down. Trial timings and format were identical to Experiment 1. On half of the trials, the “top-up” sequence ended with a 20° down-facing head and on the other half a 20° up-facing head.

Results

A full summary of up, direct, and down responses is shown in Table 2. Up- and down-oriented heads were rarely categorized as down or up, respectively; therefore,
Baseline 2 0.02 0.01 0.06 0.46 0.92
Adapt up–down 0.02 0.01 0.02 0.18 0.59
Baseline 4 0.01 0.01 0.03 0.43 0.85
Average baseline 0.01 0.01 0.04 0.44 0.88

Direct responses
Baseline 2 0.20 0.52 0.91 0.54 0.08
Adapt up–down 0.34 0.70 0.94 0.81 0.40
Baseline 4 0.25 0.54 0.94 0.56 0.15
Average baseline 0.23 0.53 0.93 0.55 0.11

Down responses
Baseline 2 0.78 0.47 0.03 0.00 0.00
Adapt up–down 0.64 0.29 0.04 0.01 0.01
Baseline 4 0.74 0.45 0.03 0.01 0.00
Average baseline 0.76 0.46 0.03 0.01 0.00

Experiment 4

Up responses
Baseline 2 0.01 0.01 0.07 0.57 0.94
Adapt direct 0.02 0.03 0.04 0.59 0.91
Baseline 4 0.00 0.01 0.03 0.46 0.79
Average baseline 0.01 0.01 0.05 0.51 0.86

Direct responses
Baseline 2 0.23 0.54 0.90 0.42 0.05
Adapt direct 0.09 0.27 0.91 0.39 0.08
Baseline 4 0.23 0.61 0.96 0.51 0.21
Average baseline 0.23 0.58 0.93 0.47 0.13

Down responses
Baseline 2 0.76 0.45 0.03 0.01 0.01
Adapt direct 0.89 0.70 0.05 0.02 0.01
Baseline 4 0.77 0.38 0.01 0.03 0.00
Average baseline 0.77 0.41 0.02 0.02 0.01

Table 2. Mean proportion of “up,” “direct,” and “down” responses to the five probe head directions in Experiments 3 and 4. “Adapt up–down” (Experiment 3) and “Adapt direct” (Experiment 4) refer to data from the top-up section of these experiments. Head orientations are labeled as follows: D10 = down 10°, D6 = down 6°, D0 = direct 0°, U6 = up 6°, and U10 = up 10°.

data are summarized as mean percentage of “direct” responses to the probe heads and adaptation was measured as the change in “direct” responses between adaptation and baseline phases. Statistical conventions were the same as for the previous two experiments.

Baseline 1 was disregarded as practice and baseline 3 was removed to eliminate any residual adaptation effects (Kloth & Schweinberger, 2008). Participants’ performance in baselines 2 and 4 (Figure 4a) were submitted to a repeated measures ANOVA examining the effects of baseline (2 and 4) and head direction (10° up, 6° up, 0°, 6° down, 10° down). Results showed significant main effect of head direction, $F(2,57, 38.61) = 66.47$, MSE = 460.51, $\eta_p^2 = 0.82$, $p < 0.001$, reflecting more accurate categorization of direct and 10° head directions than 6°. There was no main effect of baseline, $F = 1.73$, $p > 0.2$, or baseline × head direction interaction, $F < 1$. Consequently, the remaining analyses compare adaptation to the average of baselines 2 and 4.

Adaptation to an alternating sequence of heads oriented 20° up and 20° down produced an increased tendency to categorize 6° up and 6° down head directions as “direct” in the top-up phase (Figure 4b). An ANOVA comparing adaptation (average baseline, alternating up–down) with head direction showed a significant main effect of adaptation, $F(1, 15) = 35.42$, MSE = 223.81, $\eta_p^2 = 0.70$, $p < 0.001$, reflecting an overall increase in the number of “direct” responses made post-adaptation relative to baseline performance. As expected, there was a main effect of head direction, $F(2,34, 35.16) = 81.02$, MSE = 0.096, $\eta_p^2 = 0.91$, $p < 0.001$. Crucially, these main effects were qualified by a significant adaptation × head direction interaction, $F(4, 60) = 3.80$, MSE = 111.00, $\eta_p^2 = 0.20$, $p < 0.01$.

Paired $t$-tests showed a significant increase in “direct” responses to heads oriented 10° up, 6° up, 6° down, and 10° down in the top-up section of the adaptation phase relative to their baseline counterparts, up 10° $t(15) = 4.13$, up 6° $t(15) = 4.57$, down 6° $t(15) = 3.76$, and down 10° $t(15) = 3.28$, $p < 0.005$. This reflects an increased tendency to categorize heads oriented up and down as “direct” following alternating up–down adaptation. There was no significant effect for direct-facing heads, $p > 0.5$.

As in Experiment 1, the top-up adaptation sequence ended with a head oriented 20° up or 20° down on equal numbers of trials. Once again, it was important to exclude the possibility that the observed adaptation was driven by the last image in the top-up sequence. To investigate this possibility, we split the data into “end-up” and “end-down” trials and compared the proportion of “direct” responses in a two-way repeated measures ANOVA investigating final top-up image (end-up adapt and end-down adapt) and head direction. Figure 4c summarizes participants’ performance on end-left and end-right trials. As expected, the results showed a significant main effect of head direction, $F(4, 60) = 39.63$, MSE = 370.57, $\eta_p^2 = 0.73$, $p < 0.001$. However, there was no main effect of final top-up image, $F < 1$, and crucially no interaction between final top-up image and head direction, $F = 1.1$, $p > 0.3$. Hence, adaptation was not driven by the final top-up image alone.

In summary, the results of Experiment 3 show that adaptation to an alternating sequence of 20° up- and 20° down-oriented heads produced an increased tendency to categorize small angles of up- and down-oriented heads as “direct” relative to baseline performance.
Figure 4. Results of Experiments 3 and 4. For Experiment 3, the graphs show the mean percentage of “direct” responses to probes at each of the head orientations (a) in baselines 2 and 4 separately and (b) following adaptation to alternating heads oriented 20° up and heads oriented 20° down (average performance in baselines 2 and 4 is also shown) and for (c) adaptation top-up trials that ended with an up-facing adaptor and adaptation top-up trials that ended with a down-facing adaptor (average performance in baselines 2 and 4 is also shown). For Experiment 4, the graphs show the mean percentage of “direct” responses to probes at each of the head orientations (d) in baselines 2 and 4 separately and (e) following adaptation to direct-facing heads (average performance in baselines 2 and 4 is also shown). Head orientations are labeled as follows: D10 = down 10°, D6 = down 6°, D0 = direct 0°, U6 = up 6°, and U10 = up 10°. Error bars represent standard errors.
Additional analyses demonstrate that these aftereffects are not driven by the direction of the final top-up image alone.

**Experiment 4—“Direct adaptation”**

**Methods**

**Participants**

Sixteen right-handed volunteers (9 females; mean age 22.4 years ($SD = 2.78$); range 18–28 years) took part in this experiment.

**Materials**

Probe stimuli were identical to those used in Experiment 3 and adaptation stimuli comprised the stimuli with direct-oriented heads (i.e., $0^\circ$) used in Experiment 2. Adaptation and probe image sizes and visual angles were all identical to Experiment 3; sample stimuli are shown in Figure 2a.

**Design and procedure**

Experiment 4 used the same basic design as Experiments 1 to 3 (Figure 2b).

**Baseline phases**

Baseline blocks (1, 2, 3, and 4) were identical to Experiment 3.

**Adaptation phase**

The adaptation phase contained two sections (Figure 2b). Section 1 comprised a series of direct ($0^\circ$)-facing adaptor images and was identical to Experiment 2 in every respect. Section 2 featured the same probe images as used in the baseline blocks depicting heads oriented in the vertical plane, up $10^\circ$, up $6^\circ$, direct $0^\circ$, down $6^\circ$, and down $10^\circ$, and participants once again categorized them as facing “up,” “direct,” or “down.” However, identical to Experiment 2, each probe image was preceded by six direct ($0^\circ$)-facing top-up adaptor images. Trial timings for this section were identical to the previous experiments.

**Results**

Data are summarized as participants’ mean percentage of direct responses. A full summary of up, direct, and down responses is shown in Table 2.

Performance in baselines 2 and 4 (Figure 4d) were compared with an ANOVA investigating the effects of baseline (2 and 4) and head direction (up $10^\circ$, up $6^\circ$, direct $0^\circ$, down $6^\circ$, and down $10^\circ$). Results showed a significant main effect of head direction, $F(2.20, 32.98) = 59.97$, MSE = 617.26, $\eta^2_p = 0.80$, $p < 0.001$, reflecting more accurate categorization of direct and $10^\circ$ head directions than $6^\circ$. There was a main effect of baseline, $F(1.15) = 37.64$, MSE = 54.64, $\eta^2_p = 0.72$, $p < 0.001$, but the baseline x orientation interaction did not reach significance, $F(4,60) = 2.28$, $p > 0.07$. Consequently, the remaining analyses compare adaptation to the average of baselines 2 and 4, but given the main effect of baseline, the effects of adaptation are also compared to baselines 2 and 4, separately.

Following adaptation to direct-facing heads, participants showed an overall decreased tendency to categorize up- and down-facing heads as “direct” in the top-up phase relative to average baseline (Figure 4e). An ANOVA examining the effects of adaptation (average baseline, direct adapt) and head direction showed a significant main effect of adaptation, $F(1,15) = 34.64$, MSE = 126.06, $\eta^2_p = 0.70$, $p < 0.001$, reflecting a decrease in the overall number of “direct” responses made post-adaptation relative to average baseline performance. As expected, there is also a main effect of head direction, $F(2.66, 39.95) = 85.53$, MSE = 352.57, $\eta^2_p = 0.85$, $p < 0.001$. These main effects were qualified by a significant adaptation x head direction interaction, $F(4, 60) = 4.56$, MSE = 132.14, $\eta^2_p = 0.23$, $p < 0.005$. Paired t-tests showed a significant decrease in “direct” responses to down $10^\circ$ and down $6^\circ$ in the top-up phase relative to their average baseline counterparts, $D10^\circ t(15) = 3.72$, $D6^\circ t(15) = 6.40$, $ps < 0.002$. However, there was no significant difference for direct- or up-facing heads, $ps > 0.1$.

Given that the analysis comparing baselines 2 and 4 found a significant main effect of baseline, additional ANOVAs examining the effects of adaptation to direct-facing heads against baselines 2 and 4 separately were conducted (Table 3).

Paired t-tests comparing each head direction in the adaptation phase with performance on baseline 2 mirror the results from the average baseline with a significant decrease in “direct” responses to down-facing heads only ($D10^\circ t(15) = 3.62$, $p = 0.003$; $D6^\circ t(15) = 4.37$, $p = 0.001$; direct $0^\circ t(15) = 0.09$, $p = 0.9$; $U6^\circ t(15) = 0.80$, $p = 0.44$; $U10^\circ t(15) = 0.94$, $p = 0.36$). Interestingly, comparing each head direction with baseline 4 shows a reduced tendency to categorize both up- and down-facing heads as “direct” following direct adaptation ($D10^\circ t(15) = 3.09$, $p < 0.01$; $D6^\circ t(15) = 5.61$; $U6^\circ t(15) = 4.84$, $ps < 0.001$; and $U10^\circ t(15) = 2.45$, $p = 0.027$). While direct adaptation produced a reduction in “direct” responses to up-facing stimuli relative to baseline 4, paired t-tests comparing the magnitude of this effect (adapt up–down minus baseline 4 performance) show that it is significantly less marked for $6^\circ$ up probes than $6^\circ$ down probes ($t(1, 15) = 2.79$, $p <
In summary, Experiment 4 demonstrates an overall reduced tendency to categorize vertically oriented heads as “direct” following direct adaptation and this tendency is far less robust for up-facing heads relative to corresponding effect for down-facing stimuli.

**Experiments 3 and 4—Discussion**

Adaptation to an alternating sequence of 20° up- and 20° down-oriented heads (Experiment 3) produced an increased tendency to categorize small angles of up- and down-oriented heads as “direct” relative to baseline performance. Furthermore, it has been demonstrated that the effects are not driven by the direction of the final top-up image in the sequence of top-up adaptors and therefore reflect simultaneous adaptation of neural populations representing up and down head directions. In contrast, adaptation to direct (0°)-facing heads (Experiment 4) demonstrates an overall reduced tendency to categorize vertical head directions as “direct” following direct adaptation. This did not reach significance for up-facing stimuli when adaptation performance was compared to average baseline performance. However, the data show a trend toward a decreased tendency to categorize up-facing heads as “direct,” and while this trend was significant when adaptation performance is compared to performance on baseline 4, the magnitude of this effect is still less marked than the corresponding effect for down-facing stimuli. Nonetheless, the results of Experiment 4 are consistent with the predictions of multichannel coding as they show largely opposite effects of adaptation compared to Experiment 3. This may suggest that in a multichannel system coding vertical head orientations, the channel coding up-facing heads overlaps more with the direct channel than the channel coding down-facing heads (see General discussion section below).

### General discussion

Experiments 1 and 2 showed that, relative to baseline performance, adaptation to an alternating sequence of 20° left- and 20° right-oriented heads (Experiment 1) and direct-facing heads (Experiment 2) produced opposite patterns of adaptation. These opposite effects of adaptation are predicted by a multichannel-coding model. Experiments 3 and 4 provide the first demonstration of directional aftereffects for heads in the vertical plane in humans. However, whereas Experiment 3 demonstrated a clear tendency to categorize up- and down-oriented heads as direct following adaptation to alternating presentations of up and down head adaptors, the effect of adaptation to direct heads on up and down probes was less robust for up-facing heads than down-facing heads. Nonetheless, the results show largely opposite effects of adaptation to alternating up–down (Experiment 3) and direct (Experiment 4)-oriented heads, as predicted by multichannel coding. An opponent-coding model cannot accommodate such opposite findings, and therefore, our results support multichannel coding of head direction in both horizontal and vertical planes.

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<td>4.00</td>
<td>188.34</td>
<td>&lt;0.07</td>
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Table 3. Repeated measures ANOVAs comparing the effects of adaptation to direct-facing heads with baseline 2 (top) and baseline 4 (bottom).
The aftereffects reported in Experiments 1 to 4 were found across a 25% size change and changes in identity and gender between top-up adaptor and test images. This disruption to low-level visual properties and retinotopic mapping between top-up adaptor and test images means that the effects are unlikely to reflect adaptation of low-level image properties. Rather, the aftereffects are more likely to reflect adaptation of “high-level” representations of head orientation. Indeed, recent fMRI adaptation research in humans has shown that adaptation of head orientation and gaze direction occur in high-level visual areas such as STS (Calder et al., 2007; Fang, Murray, & He, 2007), providing evidence of separable coding of different head and gaze directions in this region. The human anterior STS was shown to contain distinct neural populations coding left and right gaze directions (Calder et al., 2007) and another study found identity-dependent adaptation across viewpoint in multiple face-selective areas, including right fusiform gyrus and right superior temporal sulcus (Fang, Murray, & He, 2007). In Fang et al.'s study, however, the identity of the adaptor and probe faces were the same; hence, identity-invariant coding of head direction in the STS remains to be demonstrated.

The finding that identity-invariant representations of horizontal and vertical head directions are best accounted for by a multichannel system reveals important parallels between the representation of head direction in humans and non-human primates. Single-cell recording in macaques has identified head-specific, identity-invariant cells in the STS with preferential response for up, down, full face, left, and right orientations (Perrett et al., 1985). However, it is currently unknown whether the relative engagement of just five types of cell (i.e., left, right, up, down, and direct cells) is sufficient to produce representations of all conceivable front views of others’ head direction. For example, perception of head directions such as “up-and-to-the-left” may involve conjoint activation of both “left” and “up” cells or could require yet another category of cell with a preferential response for heads oriented in this specific direction. Further adaptation studies would be required to investigate this fully.

Even if only five channels were required to represent all conceivable front-facing views of others’ head direction, this does not mean that only five pools of cells (or channels) are sufficient to represent all possible head directions. Since heads can be viewed from 360°, a simple five-channel system in humans would require each channel to be very broadly tuned; making discrimination of differences in head orientation correspondingly poor. In their single-cell investigations of macaque STS, Perrett et al. (1991) note “supernumerary” coding of view in identity-invariant cells (i.e., representations of many viewpoints in between the prototypical views necessary for recognition). It is probable that identity-invariant cells in humans that serve to represent direction of others’ attention require multiple pools of neurons tuned to many different viewpoints also. However, in order to determine the tuning width (and hence number) of channels in humans, detailed and extensive psychophysical studies would be required. Therefore, the main conclusion of the current experiments is that multichannel coding provides a more appropriate explanation of the representation of head orientation than opponent coding, which has been used to account for other high-level visual representations, such as representations of facial identity (Leopold et al., 2001; Rhodes & Jeffery, 2006).

The horizontal viewpoint aftereffects reported in Experiment 1 are consistent with previous adaptation research (Fang & He, 2005; Fang, Ijichi et al., 2007), and in Experiment 2, the finding that adapting to direct-oriented heads decreased the tendency to categorize “left”- and “right”-facing heads as direct is consistent with the recent findings showing that adapting to a frontal face can reduce face view discrimination around frontal views (Chen, Yang, Wang, & Fang, 2010). However, these studies used head images with the eyes open. Given that adaptation to left and right eye gaze has been shown to produce direction-specific eye gaze aftereffects (Calder et al., 2007; Jenkins et al., 2006), it is conceivable that previous reports of viewpoint aftereffects with heads may be partly driven by the eyes. Using head stimuli with closed eyes throughout Experiments 1 to 4 means that we can be confident that only directional information signaled by the head is contributing to these aftereffects. Such representations are comparable to those found in the macaque STS (Perrett et al., 1985), and on the basis of such single-cell recording evidence and human fMRI studies mentioned previously (Calder et al., 2007; Fang, Murray et al., 2007), we would expect that these head direction-selective cells exist in an analogous portion of human STS. In fact, Carlin et al. have recently shown that cells coding left- and right-oriented heads are located in a similar portion of anterior STS to those coding gaze direction (Calder et al., 2007; Carlin, Rowe, Kriegeskorte, Thompson, & Calder, 2011).

However, we cannot assert that the reported aftereffects arise from exclusively head-selective cells. Perrett et al. (1992) showed that a proportion of the view-selective STS cells identified in macaques responded to more than one type of directional cue (i.e., eyes, heads, and bodies) oriented in the same direction. Therefore, it is conceivable that the aftereffects reported here arise from either exclusively head-view-selective cells or view-selective cells that are invariant to cue type (i.e., respond to eyes, heads, and bodies). Detailed experiments would be required to investigate this issue. Experiment 4 examined the effect of adapting to direct-facing heads on participants’ discrimination of vertically oriented heads. The reduced tendency to categorize up-facing heads as “direct” following adaptation did not reach significance when adaptation performance was compared to average baseline performance. The data show a trend toward a decreased tendency to categorize up-facing heads as “direct,” and while this trend was
significant when adaptation performance is compared to performance on baseline 4, the magnitude of this effect is still less marked than the corresponding effect for down-facing stimuli. One potential explanation is that the experiment simply lacked power to produce significant effects for the up-facing head directions. This, however, seems unlikely as 16 participants was previously sufficient to produce robust effects (surviving Bonferroni correction), in Experiments 1, 2, and 3. Furthermore, if Experiment 4 simply lacked power, one would expect this to affect the results for both up- and down-facing head directions. While it cannot be discounted that participants’ baseline performance for up-facing stimuli in Experiment 4 was simply anomalous, it is possible that these adaptation data are revealing an asymmetry in the coding of up and down head orientations. In our baseline data (see Figure 4d and Table 2), a smaller shift from direct is required for a head to be categorized as up rather than down (i.e., 51% “up” responses to 6° up heads relative to 42% “down” responses to 6° down heads). It is therefore possible that the “up” channel shows greater overlap with the “direct” channel than the “down” channel does with the “direct” channel. If so, the crossover between the direct and up channels would be nearer the point corresponding to direct-oriented heads than the crossover between the direct and down channels (Figure 5a). It is conceivable then that although adapting to direct heads (i.e., 0°) would affect maximally the direct channel, it also produces greater adaptation of the “up” channel than the “down” channel, resulting in a smaller aftereffect for up- relative to down-facing heads (Figure 5b). Consistent with this interpretation, it is interesting to note that in Experiment 3 (Figure 4b) there is the suggestion that the magnitude of adaptation (defined as adapt U/D minus average baseline) is greater for upward- than downward-facing stimuli: a 2 x 2 ANOVA with the factors vertical direction (up, down) and orientation (6 degrees, 10 degrees) shows a borderline main effect of vertical direction, $F(1, 15) = 3.69, p = 0.074$, and no main effect of orientation or interaction ($Fs < 1$).

One psychological reason for this coding asymmetry might be the evolutionary importance of quick and accurate judgments about whether a person is looking at you or away from you. When two people are facing one another, only a small shift in head orientation upward is required for perception of where another is attending to change from “looking at you” (i.e., 0° direct) to “looking above/beyond you.” Conversely, any shift in head orientation downward from direct (0°) continues to signal attention “at you” (Figure 6). Narrow and overlapping tuning of direct and up head orientations would facilitate greater accuracy in perception of such important “at you” vs. “away from you” shifts in others’ locus of attention. While this specific interpretation is speculative, the concept of metamerism might further explain why directional cues to social attention seem to be generally coded by multichannel systems, whereas, in contrast, facial identity is thought to be opponent-coded. A metamer system is any set of detectors (or pools of neurons) with mutually overlapping tuning functions along a stimulus dimension (Howard & Rogers, 1996); hence, both multichannel- and opponent-coding systems are metameric. Metamer confusions occur when two distinct stimuli produce the same perceptual outcome (e.g., when left 2° is perceived to be the same as left 3° or when a face 70% Identity A and 75% Identity A are both perceived to be Identity A). In general, the larger the number of channels (and the narrower the tuning), the less the coding of that sensory dimension will be subject to metameric confusions. In the context of cues to social attention, accurately perceiving where someone is attending is imperative and the differences between a front-facing “at you” gaze (0°) and a 5° upward (i.e., above you) gaze could mean a matter of life and death in a predator/prey situation. Hence, we suggest that in Experiment 4 the lack of a robust aftereffect for “up”-facing head directions following “direct” adaptation might reflect closer (more overlapping) tuning of the up/direct channels than the down/direct channels (Figure 5). Practically, closer tuning
of these channels would facilitate more accurate perception of subtle shifts in attention from “at you” to “above/beyond you,” i.e., less metameric confusions would occur. More generally, perceiving the difference between 25° right and 30° right gaze/head orientation allows us to accurately determine which object people are attending to in their social world in order to be able to gauge others’ intentions toward the object and a multichannel coding system with many overlapping channels facilitates this necessity in perception. In contrast, a certain amount of metameric confusions can be an advantage in facial identity perception. For example, it is important that each time we encounter the same person we recognize them despite changes in their appearance over time (e.g., age-related changes, weight gain/loss), and an opponent-coding system, being more broadly tuned and having only two channels, would facilitate a certain degree of fluidity in perception, hence maintaining some constancy despite fluctuations in the stimulus dimension it is coding.

In conclusion, Experiments 1 to 4 demonstrate identity-invariant representations of head direction in the horizontal (left–right) and vertical (up–down) axes that are coded by a non-opponent multichannel system. Our findings reveal important parallels with single-cell recording in non-human primates (Perrett et al., 1991) and are consistent with the visual representation of other cues to direction of attention, such as eye gaze and body orientation (Calder et al., 2007; Jenkins et al., 2006; Lawson et al., 2009; Nummenmaa & Calder, 2009). Furthermore, we have demonstrated a possible asymmetry in the coding of up- and down-oriented heads and we suggest that this may facilitate accurate “at you” vs. “away from you” judgments of direction of attention, although this remains to be tested formally.

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