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Adaptation to other people's eye gaze reflects habituation of high-level perceptual representations

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ABSTRACT

Our sense of where another person is looking depends upon multiple features of their face, relating to both the deviation of their eyes and the angle of their head. In this way, gaze direction is a higher-level perceptual property that is dependent on holistic processing of lower-level visual cues. A key paradigm in social perception research is *sensory adaptation*, which has been used to probe how properties like gaze direction are encoded in the visual system. Here we test whether sensory adaptation acts on higher-level, perceptual representations of gaze direction, or occurs to lower-level visual features of the face alone. To this end, participants were adapted on faces that evoke the Wollaston illusion, in which the direction that the face appears to look differs from its veridical eye direction. We compared across sets of images that were exactly matched in the lower-level features of the face image, but perceptually distinct due to differences in the conjunction of head and eye direction. The changes in participants' perception of gaze direction following adaptation were consistent with habituation having occurred to the perceived gaze direction of the Wollaston faces, where this is dependent on integration of eye direction and head direction, rather than to lower-level sensory features of the face alone. This constitutes strong evidence for adaptable representations of other people's gaze direction in the visual system that are abstracted from lower-level facial cues.

1. Introduction

Our sense of where another person is looking depends on low-level sensory features of their eye region, relating, for example, to the geometric position of their iris and the luminance gradient across the eye (Langton, 2010). In Wollaston's illusion, however, faces with *identical eye regions* are perceived as looking in markedly different directions depending on the angle of the surrounding head (Fig. 1A) (Wollaston, 1824). This illusion vividly demonstrates that our sense of another person's direction of gaze is a *higher-order* or *holistic* perceptual property that is abstracted from lower-level sensory cues relating to eye direction and head direction. To capture the influence of head direction on perceived gaze direction, Otsuka, Mareschal, Calder, and Clifford (2014) propose a 'dual-route' model, in which head direction has two simultaneous effects in natural viewing conditions: (i) providing direct sensory cues to gaze direction, biasing perceived gaze direction *towards* the direction of the head, and (ii) altering the observer's view onto the eye region, biasing the perceived gaze direction *away* from the direction of the head (Fig. 1B) (Otsuka, Mareschal, & Clifford, 2015, 2016; Sweeny & Whitney, 2017). In the artificial context of the Wollaston illusion, the former, attractive effect causes the perceived direction of gaze to come apart from the veridical eye direction. This is because the observer's view onto the eye region remains *constant* (as a result of image editing) despite the orientation of the head being varied, thus isolating the role of head region information as a direct cue to gaze direction.

In the past decade, our visual perception of other people's direction of gaze has received increasing empirical attention as a property of our social experience that is relatively amenable to investigation. An early finding in this field was the discovery of individual cells in the anterior superior temporal sulcus (STS) of the macaque cortex that are tuned to distinct directions of gaze (Perrett et al., 1985; Perrett, Hietanen, Oram, & Benson, 1992), establishing gaze direction as a distinct property of the external world that is represented in the visual system. In humans, a key experimental paradigm that has been employed to probe the representation of gaze direction is *sensory adaptation*. In a typical adaptation paradigm, observers receive prolonged exposure to a specific direction of gaze; for instance, by viewing a series of faces with far leftwards eye direction for several minutes. This produces a robust shift in the subsequent perception of gaze direction (i.e., a high-level perceptual aftereffect), such that faces presented following adaptation are perceived as looking further to the right than they really are (i.e., the

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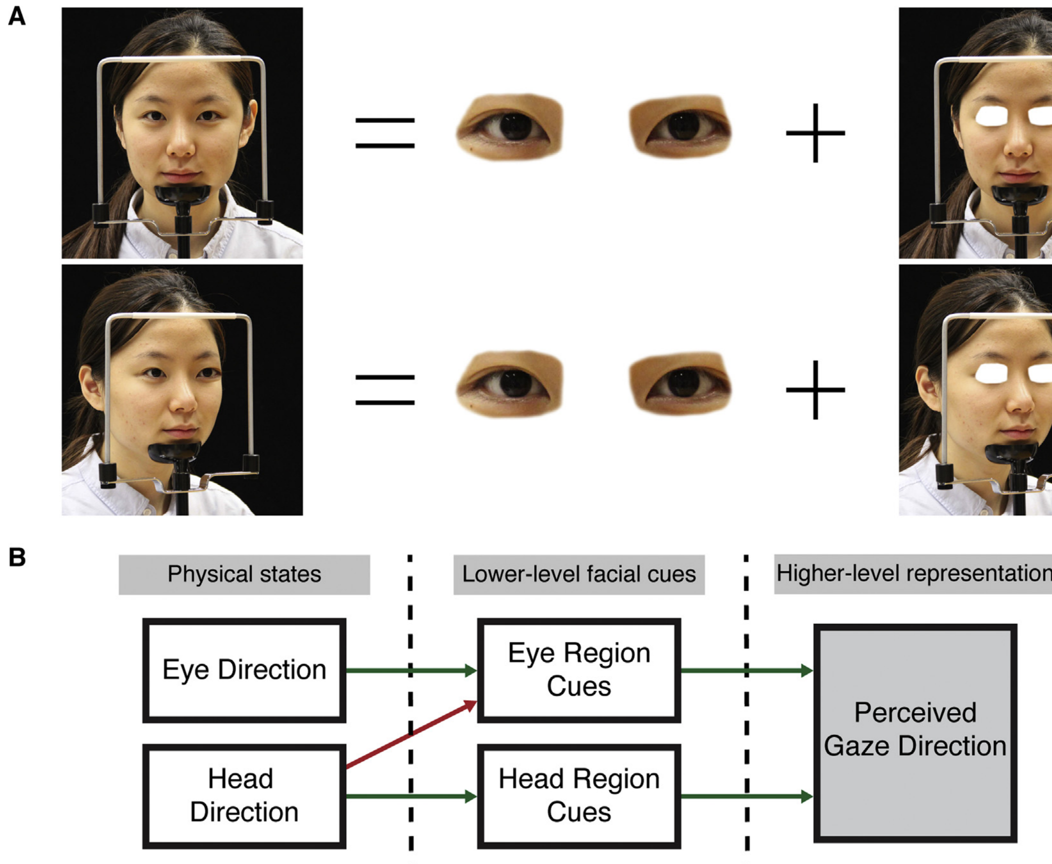

Fig. 1. (A) Wollaston's illusion. The eye region is identical across the two images, but the direction that the woman appears to be looking differs. This illustrates that our sense of where other people are looking depends on perceptual integration of head and eye cues to gaze direction, rather than lower-level features of the eye region alone. The source images used to create this demonstration of the illusion are reproduced with permission from the Columbia Gaze Data Set (Smith, Yin, Feiner, & Nayar, 2013). (B) The 'dual-route' model of perceived gaze direction, introduced in Otsuka et al. (2014). Physical states of the world, namely the head direction and eye direction of a person that we are looking at, contribute to lower-level sensory cues that our visual system can extract. This includes eye region cues (e.g., the geometry of luminance changes across the eyes) and head region cues (e.g., the contour of the nose and jaw). Different combinations of lower-level cues can produce either the same perceived gaze direction or different perceived gaze directions. In natural viewing conditions, the eye region cues to gaze direction are modulated by both eye direction and head direction, as changes in head direction alter the viewer's perspective onto the eye region. Head direction plays an additional role of providing direct cues to gaze direction. In the artificial context of the Wollaston illusion, the effect of head direction on eye region cues is controlled, such that the perceived gaze direction reflects integration of head and eye features as independent cues to where the person is looking.

perceived gaze direction is shifted away from the gaze direction that was adapted upon; Jenkins, Beaver, & Calder, 2006; Seyama & Nagayama, 2006). Adaptation effects can be modelled in terms of *population coding* in the sensory system, where the perceived direction of gaze is represented in terms of the relative activation of multiple cell populations that each have a preferred direction of gaze (Calder, Jenkins, Cassel, & Clifford, 2008; Palmer & Clifford, 2017a). The idea is that selective habituation of these cell populations, by prolonged exposure to a specific direction of gaze, causes a change in the population response to any given face stimulus and, consequently, a change in the perceived gaze direction that the stimulus evokes. The adaptation paradigm has been used to probe the functional mechanisms involved in representing other people's direction of gaze (e.g., Palmer & Clifford, 2017a; Teufel et al., 2009), the neural basis of the gaze system (e.g., Calder et al., 2007; Schweinberger, Kloth, & Jenkins, 2007), clinical differences in the effect of recent sensory history on current perception in high-level vision (e.g., Lawson, Aylward, Roiser, & Rees, 2017; Palmer, Lawson, Shankar, Clifford, & Rees, 2018), and the representation of other cues to social attention, namely head direction and body direction (e.g., Fang & He, 2005; Lawson, Clifford, & Calder, 2009; Lawson, Clifford, & Calder, 2011).

At what level of perceptual representation is habituation occurring to produce the changes in visual experience that follow adaptation to gaze direction? Gaze aftereffects are unlikely to be explained simply as reflecting adaptation to very low-level image properties (e.g., at the level of the retina or V1), as they are not abolished when differences are introduced in the low-level properties of the adapting and test stimuli, such as their location on screen, relative size, and face identity (e.g., Jenkins et al., 2006). Similarly, a recent study found that adaptation could be induced just as strongly by viewing a set of face images that maintained a *constant* direction of gaze relative to the observer, but *varied* in the combination of head and eye direction that combined to signal this direction of gaze, thus differing substantially in low-level image features (Palmer & Clifford, 2017b). Functional MRI research indicates that direction-specific effects of adaptation to eye gaze are reflected in the responses of anterior STS and parietal regions (Calder et al., 2007), and EEG studies show modulation of neural processing at 250 ms and later (Kloth & Schweinberger, 2010; Schweinberger et al., 2007). However, we saw earlier that a distinction can be made between sensory processing of face features, relating to eye direction and head direction, and the actual perceived direction of gaze evoked by a face image, where this is dependent on the integration of multiple facial cues to gaze direction. Thus, despite the importance of perceptual aftereffects to understanding of the function of the gaze system, it is yet to be established whether these effects act at the level of higher-order, perceptual representations of gaze direction (which depend on holistic