



Imagining sex and adapting to it: Different aftereffects after perceiving versus imagining faces



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ABSTRACT

A prolonged exposure (i.e., perceptual adaptation) to a male or a female face can produce changes (i.e., aftereffects) in the subsequent gender attribution of a neutral or average face, so that it appears respectively more female or more male. Studies using imagery adaptation and its aftereffects have yielded conflicting results. In the present study we used an adaptation paradigm with both imagined and perceived faces as adaptors, and assessed the aftereffects in judged masculinity/femininity when viewing an androgynous test face. We monitored eye movements and pupillary responses as a way to confirm whether participants did actively engage in visual imagery. The results indicated that both perceptual and imagery adaptation produce aftereffects, but that they run in opposite directions: a contrast effect with perception (e.g., after visual exposure to a female face, the androgynous appears as more male) and an assimilation effect with imagery (e.g., after imaginative exposure to a female face, the androgynous face appears as more female). The pupillary responses revealed dilations consistent with increased cognitive effort during the imagery phase, suggesting that the assimilation aftereffect occurred in the presence of an active and effortful mental imagery process, as also witnessed by the pattern of eye movements recorded during the imagery adaptation phase.

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1. Introduction

Many studies suggest that visual imagery involves properties and neural substrates that support visual perception (Borst & Kosslyn, 2008; Ganis, Thompson, & Kosslyn, 2004; Ishai, Ungerleider, & Haxby, 2000; Kaas et al., 2010; Kosslyn & Thompson, 2003; Kosslyn, Thompson, & Alpert, 1997; O'Craven & Kanwisher, 2000). In particular, fMRI studies have reported category-related activation during visual imagery of faces and other objects (Ishai, Ungerleider, & Haxby, 2000). For example, O'Craven and Kanwisher (2000) showed that cortical regions that are involved during visual face processing had similar selectivity during face imagery; specifically, the fusiform face area, which was more active when viewing faces than when viewing scenes, was also more active when imagining faces than when imagining scenes.

To investigate the psychological and neural mechanisms underlying perception and imagery, 'adaptation and aftereffect' studies have been largely used. It has in fact been known, at least since Aristotle's *Parva Naturalia* (see Aristotle, 2001), that the prolonged exposure to a specific feature of a stimulus alters the subsequent

perception of the same feature in an opposite direction (e.g., adapting to 'red' color engenders the aftereffect of a 'green' color). Frisby (1979) suggested that aftereffects give the psychologist a sensitive tool for probing the working of sensory mechanism. In particular, adapting to a specific level of a stimulus dimension affects only those elements that respond to that level in the given dimension, but leaves others unaffected, allowing an exploration of the selectivity in neural representation of classes of stimuli.

In the last decade, many studies have characterized the properties of these aftereffects and their implications for the perception and neural representation of complex stimuli, such as faces (Leopold et al., 2001; Webster et al., 2004; see Webster & MacLeod, 2011 for a review). Specifically, several facial attributes have been investigated with adaptation paradigms, showing that the prolonged exposure to one value of a facial attribute makes subsequently viewed neutral faces to appear as bearing an opposite value of that same attribute. For example, the sustained observation of a female face makes a subsequently presented androgynous face appear as male (Webster et al., 2004). Aftereffects have been found for many dimensions along which faces can vary naturally, including individual identity (Leopold et al., 2001), gender (Rhodes et al., 2004; Webster et al., 2004), ethnicity (Webster et al., 2004), age (O'Neil & Webster, 2011; Schweinberger et al., 2010) and expression (Cook, Matei, & Johnston, 2011; Hsu & Young, 2004; Pell

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& Richards, 2011; Rutherford, Chattha, & Krysko, 2008; Skinner & Benton, 2010; Webster et al., 2004). Thus, adaptation may play an important role to study how different attributes of the face are encoded and interpreted. In this regard, if processing during face perception and imagery activate the same cortical regions, it is also possible to ask whether and why imagery and perception adaptation would induce similar or opposite aftereffects. To date, contrasting results have been found.

Ryu, Borrmann, and Chaudhuri (2008) observed that adaptation to real or imagined faces yielded similar identity aftereffects, although those to imagined faces were reduced in magnitude. Interestingly, even not-attended faces that are processed with a minimum of attentional resources appear to produce aftereffects in facial shape (Murray, Judge, & Chen, 2012). In contrast, an ERP study by Ganis and Schendan (2008) specifically investigated adaptation effects on face versus objects during either visual imagery or perception. The authors found that both visualized and perceived adaptors (either faces or objects) affected the same neural populations by engaging the N170 component. Remarkably, imagery and perception had very different effects on these category-sensitive neural populations: a suppressive effect on the ERP signal was found with perceived adaptors and an enhancement effect was found with imagined adaptors. Behavioral results to imagined versus perceived faces similar to those of Ganis and Schendan (2008) were obtained with an adaptation study by DeBruine et al. (2010), although in the context of a sex-categorization task. In this study, the visual presentation and the imagery of faces resulted in opposite aftereffects on a test stimulus consisting of an androgynous face, respectively a “contrast effect” and an “assimilation effect” were reported. Specifically, test faces were categorized as female more often after viewing male faces than after viewing female faces. On the other hand, test faces were categorized as female more often after imagining female than male faces.

The fact that adaptation can yield opposite effects (contrast versus assimilation) depending on whether the adaptor is a physical/sensory stimulus or one that is imagined seems to point to an important distinction in how perception and imagery differ at the level of the neural substrate and/or its mode of engagement. Although there is large support that visual imagery relies upon the same neural machinery involved in perception and, indeed, can be described as a re-presentation or emulation of perception (Kosslyn, 1999), the two processes also differ in the manner the same machinery is engaged in the processing of visual information (Ganis, Thompson, & Kosslyn, 2004).

As Ganis and Schendan (2008) discuss, adaptation to perceptual stimuli would seem to be to a large extent a bottom-up process, and the typical effect (i.e. a suppression of the adapted stimulus), is likely to reflect fatigue or a refractory period after a prolonged use of the same neural network. This account is standard for explaining color afterimages, where prolonged stimulation with an object colored red will produce a ghost image of the opponent color (i.e. green), due to the imbalance in the spontaneous firing of ganglion cells, after the “red” units become refractory and are unable to excite the so-called opponent cells. Similarly, one can account for adaptation effects to dimensions of face stimuli as reflecting a suppression of neural networks coding one end of the dimension (Leopold et al., 2001; O'Toole et al., 1993), resulting in a spontaneous increase in activity of the neural network coding the other end of the same dimension (Blanz et al., 2000).

In contrast, according to Ganis and Schendan (2008), adaptation to an imagined stimulus would seem to be to a large extent a top-down driven process. Consequently one could expect opposite aftereffects, (i.e. a priming of features pertaining to the adaptor stimulus), that would exaggerate the response of the neural network to the test stimulus in the direction of the appearance of the adaptor. However, there is some controversy regarding

imagery experiments, since they may reflect artifacts due to task demands and compliance to experimental expectancy (e.g., In'tons-Peterson, 1983; Pylyshyn, 1981). In other words, assimilation may simply reflect the participants' construal that the same features of the adaptor should be prioritized at test and reported. Hence, in the present study, we not only assessed whether the sustained perception or imagery of a male or a female face reveal similar or different aftereffects in the perceived gender of a subsequently presented androgynous face, but we also sought to find evidence that participants did actively engage in visual imagery. Specifically, we reasoned that an effective manner to reveal the process of image generation is to obtain eye-tracking data during the perceptual and imagery tasks. Previous studies have shown that similar scanpaths are produced when exploring a visual display and when subsequently imagining it during both short- (Brandt & Stark, 1997; Laeng & Teodorescu, 2002) and long-term recall (Martarelli & Mast, 2013), suggesting that eye movements play a functional role in the process of visual imagery. For these reasons we explored whether the visual mental imagery of faces results in eye fixations over the same regions of the screen as those that contained salient facial parts during perception and encoding, as this information would help to determine the processes underlying both tasks. If so, a re-instatement of the eye fixations would indicate the presence of an active process of visual imagery confirming the active creation of a representation of the face. In contrast, if participants simply respond on the basis of expectations and guesses based on expectancies about the goal of the experiment, there is no reason to believe that eye fixations should resemble those of perception.

Furthermore, we argued that a difference in pupil diameter during the perception and imagery conditions would constitute additional support to the assumption that participants actively engage in mental imagery. Pupillometric changes are sensitive to perceived light level (e.g., Binda, Pereverzeva, & Murray, 2013) and to dark and bright imagined objects and scenarios (Laeng & Sulutvedt, 2014). Moreover previous studies have reported that pupil dilation reflects top-down processes, as for example during incongruent trials of the Stroop task (Laeng et al., 2011). In short-term memory experiments, the pupil diameter increases as the number of elements to be held in mind increases (Kahneman & Beatty, 1966). In general, pupil size increases as resource demands rise (Beatty, 1982; Granholm & Steinhauer, 2004; Laeng, Sirois, & Gredebäck, 2012). We therefore hypothesize that control processes and the act of representing an image within the neural networks supporting facial information would tax the cognitive system to a larger extent than simply fixating a visual stimulus (during perceptual adaptation). Therefore, we predicted that pupillary diameter should be greater during imagery adaptation than perceptual adaptation due to the increased mental effort provoked by the deliberate act of conjuring up a visual image.

2. Methods

2.1. Participants

Twenty-seven participants (18 females; mean age: 23.55) were recruited from the Psychology Department at the University of Oslo. All participants had normal or corrected-to-normal vision (with contact lenses). They were rewarded for their participation by means of a gift voucher worth 100 Norwegian Crowns.

2.2. Stimuli

All stimuli were frontal-view images of individual faces showing a neutral expression. Six “adaptation” stimuli were obtained

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