



Watching the brain recalibrate: Neural correlates of renormalization during face adaptation



Nadine Kloth^{a,b,*}, Gillian Rhodes^{a,b}, Stefan R. Schweinberger^{a,b}

^a ARC Centre of Excellence in Cognition and its Disorders, School of Psychology, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

^b DFG Research Unit Person Perception, Department of Psychology, Friedrich Schiller University of Jena, Leutragraben 1, 07743 Jena, Germany

ARTICLE INFO

Keywords:

Face distortion aftereffect
Event-related potentials
Opponent coding
Multichannel coding
N170
P2

ABSTRACT

The face perception system flexibly adjusts its neural responses to current face exposure, inducing aftereffects in the perception of subsequent faces. For instance, adaptation to expanded faces makes undistorted faces appear compressed, and adaptation to compressed faces makes undistorted faces appear expanded. Such distortion aftereffects have been proposed to result from renormalization, in which the visual system constantly updates a prototype according to the adaptors' characteristics and evaluates subsequent faces relative to that. However, although consequences of adaptation are easily observed in behavioral aftereffects, it has proven difficult to observe renormalization during adaptation itself. Here we directly measured brain responses during adaptation to establish a neural correlate of renormalization. Given that the face-evoked occipito-temporal P2 event-related brain potential has been found to increase with face prototypicality, we reasoned that the adaptor-elicited P2 could serve as an electrophysiological indicator for renormalization. Participants adapted to sequences of four distorted (compressed or expanded) or undistorted faces, followed by a slightly distorted test face, which they had to classify as undistorted or distorted. We analysed ERPs evoked by each of the adaptors and found that P2 (but not N170) amplitudes evoked by consecutive adaptor faces exhibited an electrophysiological pattern of renormalization during adaptation to distorted faces: P2 amplitudes evoked by both compressed and expanded adaptors significantly increased towards asymptotic levels as adaptation proceeded. P2 amplitudes were smallest for the first adaptor, significantly larger for the second, and yet larger for the third adaptor. We conclude that the sensitivity of the occipito-temporal P2 to the perceived deviation of a face from the norm makes this component an excellent tool to study adaptation-induced renormalization.

Introduction

Face adaptation is the recalibration of response properties of face-sensitive neurons to the faces we experience. Adaptation induces aftereffects, that is, biases in the perception of subsequently presented faces (Clifford and Rhodes, 2005). For instance, adaptation to expanded faces biases observers to subsequently perceive faces as compressed, making them judge slightly expanded faces as more normal-looking than before adaptation (face distortion aftereffect, Webster and MacLin, 1999). Such contrastive aftereffects also occur after adaptation to other face characteristics, such as identity, sex, ethnicity, age, or gaze direction (Leopold et al., 2001; Webster et al., 2004; Jenkins et al., 2006; Schweinberger et al., 2010; for a review, see Webster and MacLeod, 2011).

Experimental adaptation paradigms have been used to study face coding mechanisms (Clifford and Rhodes, 2005; Webster, 2011;

Webster and MacLeod, 2011). Two types of coding generally exist in the visual system: opponent and multichannel coding (Webster and MacLeod, 2011). In opponent coding, two sets of neural channels selectively respond to opposite ends of a stimulus dimension (e.g., compression vs. expansion on a spatial configuration dimension). Their differential output determines the percept. The stimulus quality at which both channels respond equally has a special status; it serves as a norm or prototype. Adaptation updates this norm, shifting it towards the direction of the adaptors and hence making the adaptors appear more normal. For instance, when predominantly exposed to expanded faces, the expansion-sensitive channel adapts and becomes less responsive, causing a shift of the equilibrium point towards expansion. Relative to this more expanded norm, a face previously perceived as undistorted now appears compressed. In contrast, multichannel models typically have multiple narrowly tuned channels, each coding a certain range of characteristics on a given dimension. In the example of

* Correspondence to: School of Psychology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
E-mail address: nadine.kloth@uwa.edu.au (N. Kloth).

coding spatial configurations, one channel might respond to very compressed faces, another to slightly compressed faces, another to undistorted faces, yet another to slightly expanded faces, etc. Adaptation to an expanded face reduces activity in the channel most sensitive to that degree of expansion, and possibly, to a smaller extent, that in neighboring channels as well. Consequently, the unadapted channels sensitive to compression dominate the overall activity of the perceptual system after adaptation, also explaining the contrastive aftereffect. Importantly, there is no channel with a special status or a norm in a multichannel system.

The nature of the neural coding of different face attributes has been investigated in various behavioral studies, using experimental manipulations for which the two coding types make different predictions. Such paradigms include studying the effects of increasing adaptor strengths on the size of the aftereffect (McKone et al., 2014, 2015; Pond et al., 2013; Zhao et al., 2011), or comparing the effect of adaptation to neutral stimuli to alternating adaptation to opposite adaptors (Burton et al., 2015; Calder et al., 2008). For some face attributes, the neural coding mechanisms could be established with reasonable confidence. Gaze direction, for instance, appears to be coded in a three-channel system (Calder et al., 2008; but see Kloth and Schweinberger, 2010), whereas facial configurations, and emotional expressions, seem to be opponent coded (Burton et al., 2013; Leopold et al., 2001; Robbins et al., 2007; Skinner and Benton, 2010; Storrs and Arnold, 2012; Webster and MacLin, 1999). However, the nature of the neural coding of other face attributes, like face sex or face identity, is still a matter of heated debate (Jeffery et al., 2011; McKone et al., 2014, 2015; Pond et al., 2013; Rhodes and Jeffery, 2006; Storrs and Arnold, 2012, 2015; Zhao et al., 2011).

Behavioral studies trying to distinguish between neural coding models face several challenges, which can be broadly summarized as difficulties to infer neural mechanisms from behavioral response patterns. First, it has been claimed that aftereffect patterns do not directly map onto coding systems, and that both types of model can account for many aftereffect patterns (Ross et al., 2014). Second, behavioral aftereffects might not solely indicate changes in perceptual processing, but could also reflect contributions of cognitive biases and response heuristics (Ross et al., 2014; Storrs, 2015). Third, predictions derived from single dimensions, as tested in many studies, may not “scale up” to more complex multi-dimensional face spaces (Ross et al., 2014). Finally, complex visual stimuli, like human faces, are processed on various levels of the visual system, for all of which adaptive coding is also known to occur. It is unlikely that the same type of coding mechanism is used throughout; rather, different stimulus aspects are coded on different levels of the visual system, possibly using different coding strategies. For instance, faces also contain comparably simple visual properties, like luminance, contrast, color, and line orientations, all of which the visual system will adapt to on lower levels as well. Face aftereffects could therefore potentially originate from many levels of visual processing and it is possible that contributions of such low-level aftereffects affect the pattern of effects observed in face adaptation studies, and therefore bias the interpretation of the nature of the neural coding of an assumed high-level aftereffect (Dennett et al., 2012; see Pond et al., 2013, for a discussion of how contributions of uncontrolled color aftereffects might affect the interpretation of the neural coding of face sex on high levels of the visual system).

Here, we tried to circumvent some of these methodological challenges by establishing a novel event-related brain potentials (ERPs) paradigm to trace neural processing during adaptation. In this specific context, ERPs have three benefits. First, they measure neuronal activity, meaning that they might help trace neural adaptation as it occurs, therefore nicely complementing behavioral adaptation paradigms, which infer neural adaptation from behavioral responses. Second, the high temporal resolution of ERPs can provide some insight into the processing stage (e.g., low- vs. high-level perceptual, post-perceptual, or decisional) at which the observed effects occur.

Specifically, the use of ERPs allows us to focus on adaptation-induced changes of face processing in a time window in which high-level face processing is known to occur, therefore reducing potential effects of low-level adaptation and post-perceptual cognitive strategies such as response biases. Third, ERPs are sensitive to a face's normality or prototypicality, which makes them ideally suited to uncover renormalization during adaptation.

The prediction of renormalization, i.e., a shift of the equilibrium point between opponent channels towards the adaptor which leads to the adaptor appearing more normal, is central to opponent coding models, but is absent from multichannel models. Evidence for renormalization might therefore be ideally suited to differentiate between the two types of neural coding. Unfortunately, renormalization has proven difficult to demonstrate in behavioral studies (see Storrs and Arnold, 2012, for partial evidence of renormalization during adaptation to face distortions). However, a neural correlate of adaptation-induced increased perceived normality of *test* faces in face distortion aftereffects has been found in the occipito-temporal P2 component (Burkhardt et al., 2010). The occipito-temporal P2 is a positive-going ERP 200–250 ms after face onset that is larger for more typical than less typical faces (Halit et al., 2000; Zheng et al., 2012) and is thought to reflect the encoding of a face's second order spatial configuration relative to a prototype (Latinus and Taylor, 2006), preceding face identification (for a recent review on the functional significance of face-elicited ERP components, see Schweinberger and Neumann, 2016). Burkhardt et al. (2010) have shown that, before adaptation, undistorted test faces induced larger P2 amplitudes at occipito-temporal sites than distorted faces. After adaptation to consistently distorted faces, test faces with low levels of the adapted distortion evoked larger P2 responses than undistorted faces. Moreover, previous studies reported more pronounced P2 amplitudes for typical than distinctive faces (Schulz et al., 2012a), for anti-caricatured than veridical faces (Schulz et al., 2012b), for faces with low-identity strength than with high identity-strength (Zheng et al., 2012), for own-race than other-race faces (Stahl et al., 2008; Wiese et al., 2014), and for young than old faces in young observers (Wiese et al., 2008). While these findings could partly reflect an increased occipito-temporal negativity for perceptually distinctive faces that overlaps in time with the P2 (for relevant findings, cf. Faerber et al., 2015), the relevant aspect for present purposes is that the occipito-temporal P2 consistently indicates a face's perceived normality.

The present study aims at establishing whether P2 amplitude can also serve as an indicator of ongoing renormalization *during* adaptation. Based on earlier evidence that P2 amplitudes signal the perceived normality of a face, we predicted that ongoing renormalization should be reflected by an increase in P2 amplitudes evoked by consecutive adaptors. We tested this hypothesis studying the face distortion aftereffect, because converging evidence from various different behavioral paradigms strongly suggests that face distortions are coded in an opponent system (Webster and MacLin, 1999; Robbins et al., 2007; Storrs and Arnold, 2012), and one would therefore predict renormalization during adaptation to face distortions. We alternated trials showing compressed, undistorted, and expanded adaptors. In each trial, four different adaptor identities with equivalent distortions were presented consecutively, followed by a slightly compressed or slightly expanded test face, which participants had to classify as distorted or normal-looking. We predicted that ongoing renormalization during adaptation would be reflected by a systematic increase in adaptor-evoked P2 amplitudes, with larger P2 amplitudes evoked by adaptors later in the adaptation sequence. We also measured ERPs evoked by test faces. For these, we expected to replicate Burkhardt et al. (2010) findings of enhanced P2 amplitudes for test faces showing the same distortion as the preceding adaptors. Finally, to establish the extent to which any potential effects of adaptation observed in the P2 component might be carried over from the preceding N170 time window, we also examined effects of adaptation on the N170 evoked by test faces.

متن کامل مقاله

دریافت فوری ←

ISIArticles

مرجع مقالات تخصصی ایران

- ✓ امکان دانلود نسخه تمام متن مقالات انگلیسی
- ✓ امکان دانلود نسخه ترجمه شده مقالات
- ✓ پذیرش سفارش ترجمه تخصصی
- ✓ امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
- ✓ امکان دانلود رایگان ۲ صفحه اول هر مقاله
- ✓ امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
- ✓ دانلود فوری مقاله پس از پرداخت آنلاین
- ✓ پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات