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Research Report

Afterimage induced neural activity during emotional face perception

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ABSTRACT

The N170 response differs when positive versus negative facial expressions are viewed. This neural response could be associated with the perception of emotions, or some feature of the stimulus. We used an aftereffect paradigm to clarify. Consistent with previous reports of emotional aftereffects, a neutral face was more likely to be described as happy following a sad face adaptation, and more likely to be described as sad following a happy face adaptation. In addition, similar to previous observations with actual emotional faces, we found differences in the latency of the N170 elicited by the neutral face following sad versus happy face adaptation, demonstrating that the emotion-specific effect on the N170 emerges even when emotion expressions are perceptually different but physically identical. The re-entry of emotional information from other brain regions may be driving the emotional aftereffects and the N170 latency differences.

1. Introduction

The early face-sensitive event-related potential (ERP) component N170 (Bentin et al., 1996; Botzel et al., 1995; Itier and Taylor, 2004; Rossion et al., 2000; Rousselet et al., 2004) peaks later for negative emotions compared to positive emotions (Batty and Taylor, 2003), suggesting that the N170 is sensitive to different types of emotions. However, it is unclear whether this difference in brain response to positive and negative faces reflects the *perception* of happy and sad faces, or whether the difference is stimulus-driven. The emotion aftereffects paradigm can help distinguish these two possibilities.

1.1. *Visual aftereffects*

Visual aftereffects reflect short-term changes in the perception of a visual stimulus following the fixation of an adapting stimulus. For example, with color aftereffects, a white square is perceived as red following fixation of an adapting green square (Webster and Mollon, 1991). Fixating on a face can create visual aftereffects, whereby the perception of a face is influenced by previously viewed faces (Leopold et al., 2005; Webster and MacLin, 1999; Watson and Clifford, 2003). Face aftereffects have been found in the perception of attractiveness (Rhodes et al., 2003), gender (Davidenko et al., 2006; Little

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et al., 2008, 2005; Jaquet and Rhodes, 2008), race (Jaquet et al., 2008; Little et al., 2008), age (Little et al., 2008), and emotion (Rutherford et al., 2008; Russell and Fehr, 1987; Hsu and Young, 2004; Benton and Burgess, 2008).

1.2. Emotion aftereffects

Emotional facial expressions produce aftereffects: The same neutral face is perceived as sad following fixation of an adapting happy face and perceived as happy following fixation of an adapting sad face. Fixating on a facial expression can change both the category and the intensity rating of subsequently viewed facial expressions (Russell and Fehr, 1987). It has been proposed that facial aftereffects are not simply produced by adaptation to low-level individual elements of the face, but rather adaptation of higher-level neural representations of faces and emotional expressions (Butler et al., 2008).

1.3. ERP correlates of emotional facial expressions

There are latency and amplitude differences in the ERP neural response that distinguish between processing of positive and negative images, including distinguishing emotional facial expressions (Krolak-Salmon et al., 2001; Luo et al., 2010). Both the P1 and the N230 are larger in amplitude for emotionally expressive faces compared to neutral faces (Balconi and Pozzoli, 2003; Batty and Taylor, 2003), and the early posterior negativity (EPN) is larger in response to emotional stimuli (Schupp et al., 2003, 2004b, 2013). There is also evidence of sensitivity to emotional stimuli at later stages of processing: the late positive potential (LPP) and the late positive component (LPC), which have similar latency and topography over medial parietal cortex, are greater in amplitude for emotional stimuli (positive and negative) compared to neutral stimuli (Cuthbert et al., 2000; Hajcak and Olvet, 2008; Johnston et al., 1986; Moser et al., 2006; Schupp et al., 2003, 2004b, 2013; Weinberg and Hajcak, 2010). Moreover, some studies have found enhanced responses for negative images compared with positive images (Hajcak and Olvet, 2008; Huang and Luo, 2006; Ito and Cacioppo, 2000), suggesting that the late positive components are sensitive to the valence of the emotional stimulus, demonstrating a possible negativity bias or sensitivity to biological imperatives such as threat (Weinberg and Hajcak, 2010).

The N170 component, which has been useful as an index for structural face processing, also differs across expressive faces compared to neutral faces, and across categories of emotional facial expressions (Batty and Taylor, 2003). More important to the current study, Batty and Taylor (2003) showed that the latency of the N170 increased for negative emotions compared to positive emotions, and although the amplitude of the N170 did not differ among specific emotional expressions, the main effect of emotion was driven by a larger N170 amplitude for fearful faces. These results suggest that the processing of different types of emotions, i.e., positive vs. negative, can be differentiated based on early face sensitive ERP components. The question is whether this is due to stimulus driven differences in the processing of emotional faces or to actual differences in perception. This is an important question because it speaks to the hypothesis that emotion aftereffects incorporate feedback from higher levels of emotion processing, and the possibility that this leads to modulation of early stimulus driven processing at the N170.

1.4. The current study

When interpreting ERP responses to an emotional stimulus, it is difficult to separate contributions from stimulus-driven vs. perceptually-driven processes because the stimulus itself is the emotional trigger for perception. The current study used the aftereffect paradigm to examine the ERP response to neutral faces following adaptation to a happy versus sad face. This provided a direct test of the two competing hypotheses: on the one hand, it is possible that the previously reported ERP differences between happy and sad faces are stimulus-driven. If this were true, brain responses would be the same to all exposures to the neutral faces regardless of perceptual differences induced by fixating an emotional facial expression. On the other hand, the differences in brain response might be associated with the perceived positive or negative emotion, in which case, the brain would respond differently to viewing the same neutral face when the aftereffect induced a happy versus sad perception. Participants were adapted to either a happy or sad facial expression for 45 s. Immediately after adaptation, a neutral expression of the same individual was briefly presented and participants were asked to label the emotion of the second face via a key press. The current study is the first that we are aware of to investigate the ERP correlates of emotional facial aftereffects. Note that because we are using an aftereffect paradigm, the ERP protocol departs from the typical protocol in that the inter-stimulus interval (ISI) between the adapting stimulus and the probe stimulus is zero. The reason for not including an ISI in an aftereffect paradigm is that the afterimage effect is fleeting and susceptible to interference: any visual stimulus onset or offset occurring just prior to the test image could interfere with the effect as they have been shown to decrease rapidly with increased test trial duration (Leopold et al., 2005). Our zero ISI does not provide a strong enough visual onset to trigger reliable early visual evoked potentials (e.g. P1), but we do expect to observe emotional facial changes at the N170 and LPC components.

2. Experimental procedures

2.1. Participants

Participants were 22 undergraduate students (13 females) whose average age was 19.6 years (SD=1.98). Participants were recruited through first-year psychology classes at McMaster University and received partial course credit. All had normal or corrected to normal vision.

2.2. Materials

2.2.1. Apparatus

Stimuli were presented and participants' responses were collected with Presentation® experimental software (Version

12.1), running on a PC computer with Windows XP operating system. The display used was a 17-in. monitor, at refresh rate of 75 Hz. The display was viewed binocularly at a distance of 90 cm and participants used a chin rest to maintain this distance throughout the experiment. Participants responded by pressing one of four keys on the keyboard (z, x,., or/).

2.2.2. *Stimuli*

Eighteen greyscale photographs of faces displaying happiness (nine male models), 18 greyscale photographs of faces displaying sadness (nine male models), and 18 greyscale photographs of neutral expressions (nine male models) were used as adapting stimuli and test stimuli. All photographs were taken from the Ekman and Friesen (1976) *Pictures of Facial Affect* set. Photographs were displayed at of 9.1° of visual angle high and 6.3° of visual angle wide.

2.3. *Behavioural procedure*

Participants were seated in front of the monitor and verbal instructions were given. There were 20 practice trials in which the words “happy”, “slightly happy”, “slightly sad”, or “sad” appeared on the screen until the participant responded with the correct key press. These trials were included to ensure participants understood the correct key presses corresponding to each descriptive word before proceeding to the test trials. Each test trial began with a 1 s central fixation-cross. The adapting stimulus was presented for 45 s duration and then immediately followed by the probe (800 ms duration). Participants chose an emotion term (happy, slightly happy, slightly sad, or sad) to describe the probe stimulus by pressing a key. The next trial was initiated by the participant′s response to the probe stimulus.

The development of any visual aftereffect takes several seconds (Wede and Francis, 2006). Similarly, in order to create a face afterimage, an observer has to fixate a face image for many seconds to get an effect, and the effect strengthens with time (Rhodes et al., 2007). In the study of emotional facial expressions, a 45- to 60-s adaptation has been used previously (Rutherford et al., 2008, 2012; Pell and Richards, 2011; Skinner and Benton, 2010) although some experiments use a shorter fixation such as 5 s (Butler et al., 2008; Campbell and Burke, 2009; Vida and Mondloch, 2009). The ERP averages are constructed from many observations elicited by presentation of happy and sad adaptation images mixed randomly within a block; this random presentation is critical to avoid expectations on upcoming trials, however, it also means that participants are switching many times between happy and sad adaptations. Thus, we used the longer 45-s duration to ensure that we would observe aftereffects on each trial.

The experimental block included 60 unique trials presented in random order. Participants were given the opportunity to take a short break after every 15 trials throughout the experiment. There were 36 experimental trials in which an emotional adapting image (18 happy, 18 sad) was followed by a neutral probe. There were also 18 control trials in which both adapting and probe images were the same neutral image (mirror reversed), and 6 diversion trials in which a neutral adapting image was followed by an emotional probe image. These trials were included to prevent participants from realizing that every second image in a trial pair was a neutral face. These trials also served as a check of participants′ accuracy. For all trials, the adapting and probe images were of the same individual. While it is typical for experiments using ERP analysis to include more trials per participant, the nature of aftereffect trials (each 46 s in length) extended the length of the session requiring a balance between participant fatigue and data quality. The experimental session took approximately 1.5 h to complete.

Table 1 – Number of trials per condition for each participant included in the ERP analyses. Selected trials were those for which the participant experienced the emotional aftereffect (neutral probe perceived as happy following a sad adapting face or neutral probe perceived as sad following a happy adapting face) as well as the neutral control condition (neutral adapting face).

	Adapting image		
Participant	Happy	Sad	Neutral
1	14	15	18
2	11	9	18
3	14	13	18
4	17	8	18
5	14	15	18
6	14	15	17
7	15	16	18
8	14	14	17
9	13	15	17
10	14	11	18
11	15	15	18
12	6	14	18
13	12	9	17
14	16	12	18
15	13	13	18
16	12	13	17
17	12	9	17
18	12	17	17
19	16	12	17
20	12	13	18
21	12	13	17
22	15	14	18

2.4. *EEG acquisition and analysis*

The ERP analysis was conducted on neutral probe trials, including those following the neutral adapting image (control) and those in which participants experienced the emotional aftereffect (i.e., sad perception following happy adapting image and happy perception following sad adapting image). The ActiveTwo Biosemi system was used to record continuous EEG activity from 128 Ag/AgCl scalp electrodes plus four additional electrodes placed at the outer canthi and just below each eye for recording horizontal and vertical eye movements. Two additional electrodes, common mode sense (CMS) active electrode and driven right leg (DRL) passive electrode were also used (http://www.biosemi.com/faq/cms&drl.htm). The continuous signal was acquired with an open pass-band from DC to 150 Hz and digitized at 512 Hz. The continuous EEG signal was bandpass filtered between 0.1 Hz and 55 Hz and re-referenced to a common average reference. Data were segmented into 1000 ms epochs with a 100 ms pre-stimulus baseline. Preliminary artefact removal was performed using independent component analysis (ICA) as implemented in EEGLAB software (Delorme and Makeig, 2004). Trials contaminated with excessive amplitudes were removed first; the mean proportion of rejected trials was .02±.03 *SD*. Then ICA decomposition was performed on the remaining concatenated trials, and ICA components carrying ocular and muscle artefacts were subtracted from the data. This resulted in a total of 293 and 285 neutral faces perceived as happy and sad, respectively (Table 1 displays the total number of trials for each condition per participant). Although this is a relatively low number of trials than typically included in ERP analyses, due to the long duration of the adapting trials, the design of the experiment allowed us to measure the neural response during emotional aftereffects.

3. Results

3.1. *Behavioural results*

We examined whether the expression of the adapting image influenced participants' categorization of the same neutral probe face. We collapsed participants' responses into happy (which included happy and slightly happy responses) and sad (which included sad and slightly sad responses) categories (Table 2 shows the proportions for all four categories). When participants viewed a happy adapting image, they were more likely to label the neutral probe image as sad ($M=.733$, $SD=.141$) than happy ($M=.267$, $SD=.141$). In contrast, when participants viewed a sad adapting image, they were more likely to perceive the neutral probe image as happy ($M=.764$, $SD=.127$) than sad ($M=.236$, $SD=.127$). Thus, behavioural results show a strong effect of adapting image type, as illustrated in Fig. 1. These observations were supported by a repeated measures ANOVA on the proportion of trials participants perceived the neutral probe as happy or sad with two within-subject factors of adapting emotion (happy vs. sad vs. neutral) and perceived emotion of neutral probe (happy vs. sad), which revealed a significant interaction between adapting emotion and perceived emotion of neutral probe, $F(1,22)=70.06$, $p<.001$, $d=3.57$. Post hoc paired samples t tests contrasting happy versus sad responses for each adapting emotion revealed a significant difference between happy versus sad responses for the happy adapting expression ($t(21)=-7.718$, $p<.001$, $d=3.37$) and the sad adapting expression ($t(21)=9.736$, $p<.001$, $d=4.25$), but not for the neutral adapting expression ($t(21)=1.650$, $p=.114$, $d=.72$). No other effects were significant.

3.2. *N170 and early posterior negativity (EPN) results*

As depicted in Fig. 2, the N170 component displayed maximal peak amplitude at electrodes over occipital–parietal cortex at electrode locations P7/P8 and PO7/PO8, consistent with N170 topography in the literature (Rossion and Jacques, 2008). Using the grand average waveform as a guide, we extracted subject-specific peak amplitude and latency values for the N170 component at electrodes P7/P8 and PO7/PO8 by identifying the minimum point between 180 ms and 218 ms (means and standard errors corrected for repeated-measures are presented in Table 3). We computed separate repeated measures ANOVAs for peak amplitude and latency with three within-subject factors of emotional afterimage (happy perception following sad adapting image vs. sad perception following happy adapting image vs. neutral control), hemisphere (right vs. left), and electrode position (parietal: P7, P8 vs. occipital–parietal: PO7, PO8). Fig. 2 provides a topographical voltage plot, showing the typical N170 spatial distribution. As can be seen in Fig. 2, the peak amplitude of the N170 component was larger over the right hemisphere than the left hemisphere, evidenced by a main effect of hemisphere for amplitude [$F(1,21)=15.09$, $p<.01$, partial $\eta^2=.42$]. The interaction between emotional afterimage and hemisphere was not

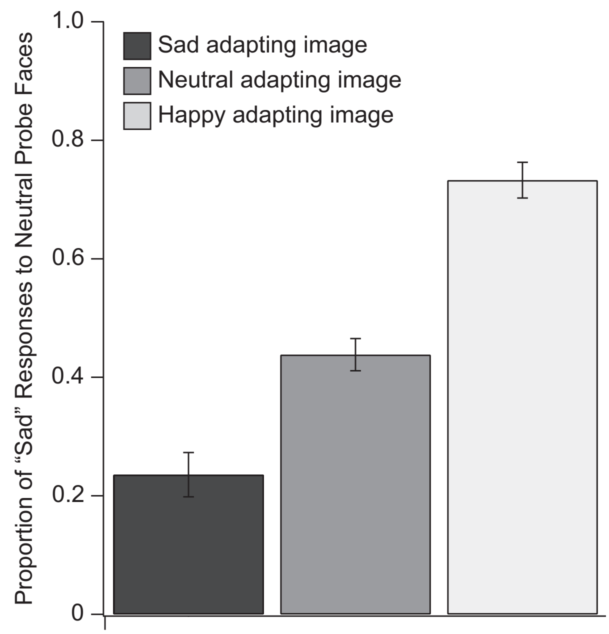

Fig. 1 – Proportion of "sad" responses made to the neutral face after adapting to either a sad, neutral or happy facial expression. Chance categorization is .50, meaning that participants were equally likely to respond "sad" or "happy". The emotional aftereffect is demonstrated following adaptation to a sad face (the neutral face was more likely to be perceived happy) and a happy face (the neutral face was more likely to be perceived as sad). Adaptation to a neutral face produced performance near chance; that is, no emotional aftereffect.

Table 2 – Proportion responses to neutral faces following adaptation to an emotional face.

	Happy	Slightly happy	Slightly sad	Sad
Neutral faces preceded by a happy face	0.01	0.25	0.62	0.12
Neutral faces preceded by a sad face	0.04	0.68	0.25	0.03
Neutral faces preceded by a neutral face	0.02	0.51	0.42	0.05

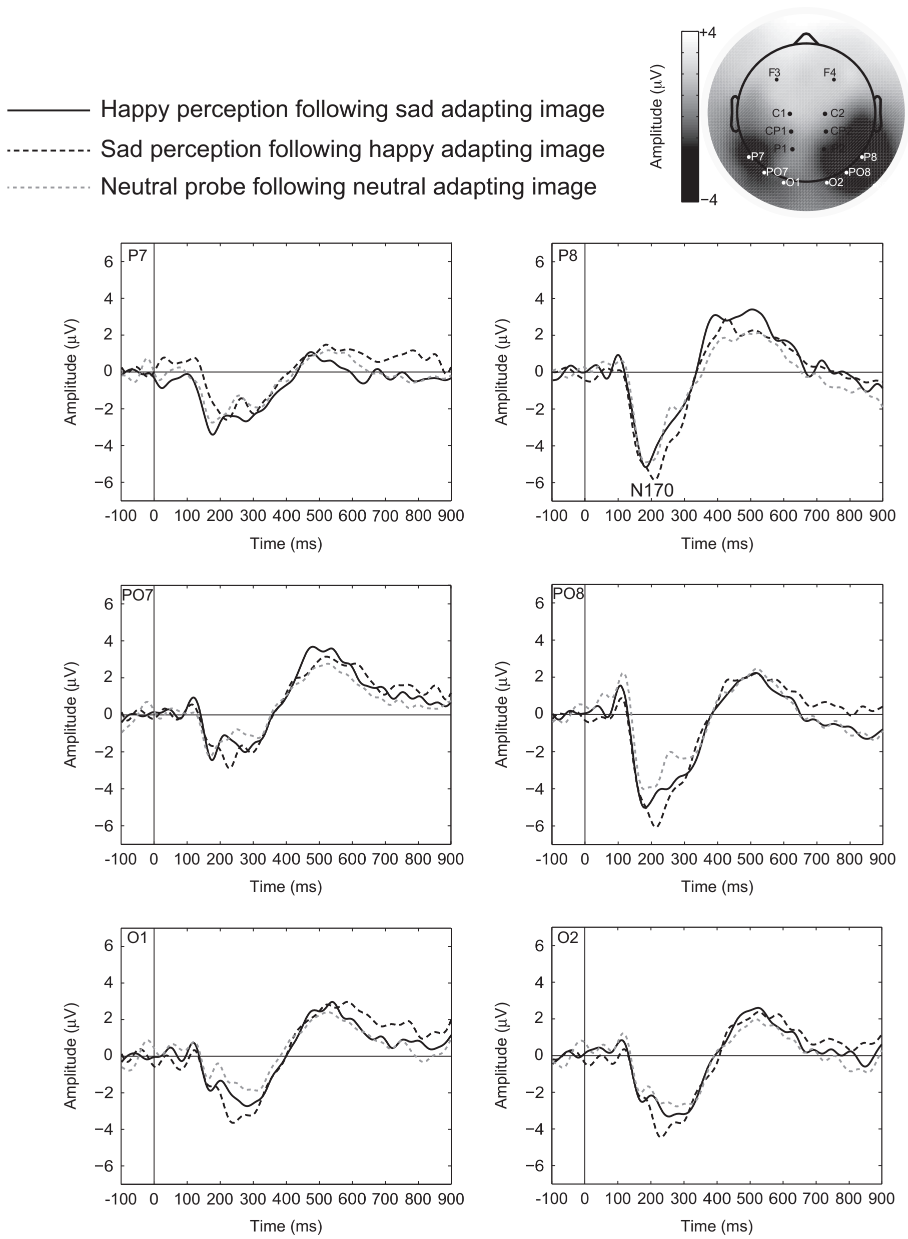

Fig. 2 – Event-related potential waveforms for occipital (O1, O2) and occipital–parietal sites (PO7, PO8, P7, P8) in response to neutral probes following happy, sad, or neutral adapting images. Waveforms consist of averages for which the behavioral adaptation effect occurred (neutral probes were perceived as happy following sad adapting images or neutral probes were perceived as sad following happy adapting images). Neutral adapting images represent the control condition in which a neutral face was primed by the mirrored-image of the same neutral face; averages include both happy and sad responses. We applied a lowpass filter of 20 Hz to the grand averaged waveforms for visualization purpose only. Topographical head plot captures the spatial distribution of the N170 component at 185 ms post-stimulus onset in response to neural faces that were perceived as happy or sad.

significant [$F(2,42)=1.73$, $p=.19$], and no other amplitude differences were significant. Although there were small amplitude differences in the N170 at PO8, the main effect for emotional afterimage was not significant [$F(2,42)=1.41$, $p=.26$].

As illustrated in Fig. 4, the N170 component peaked earlier for happy afterimages compared to sad afterimages; neutral control trials elicited an intermediate N170 peak latency. This observation was supported by a main effect of emotional afterimage for latency [$F(2,42)=3.79$, $p<.05$, partial $\eta^2=.15$]. Post hoc pairwise comparisons adjusted for multiple comparisons (least significant differences) revealed that happy afterimages peaked earlier than sad afterimages ($p=.008$). No other latency differences were significant.

We also inspected a 200–300 ms time window at lateral occipital sites (P7/P8 and PO7/PO8) where we might expect to

Table 3 – Mean (corrected standard error) for N170 peak amplitude (μV) and latency (ms).

		Left hemisphere		*Right hemisphere*	
		P7	PO7	P8	PO8
Amplitude	Happy afterimage	−4.90 (.53)	−3.81 (.37)	−6.32 (.34)	−6.43 (.45)
	Neutral afterimage	−4.30 (.64)	−3.36 (.62)	−6.47 (.86)	−5.92 (.46)
	Sad afterimage	−4.13 (.63)	−3.97 (.60)	−7.43 (.64)	−7.67 (.61)
Latency	Happy afterimage	196 (2)	197 (2)	199 (3)	197 (2)
	Neutral afterimage	204 (2)	202 (2)	201 (3)	201 (3)
	Sad afterimage	205 (3)	205 (3)	202 (3)	206 (3)

see effects of emotional processing on the amplitude of the EPN (Schupp et al., 2004a, 2004b, 2013). Repeated measures ANOVA for EPN amplitude (emotional afterimage: happy perception following sad adapting image vs. sad perception following happy adapting image vs. neutral control) and hemisphere (right vs. left) revealed no significant differences for emotional afterimage [$F(2,42)=1.34$, $p=.27$], hemisphere [$F(1,21)=1.27$, $p=.27$], or the interaction [$F(2,42)=0.61$, $p=.55$].

3.3. *Late positive potential (LPP) and mid-latency frontal component results*

Two sets of analyses on mean amplitude were performed at frontal electrode sites (F3/Fz/F4) and central parietal sites (C1/Cz/C2, CP1/CPz/CP2, P1/Pz/P2) in order to test the effects of the two within-subject factors: emotional afterimage (happy perception following sad adapting image vs. sad perception following happy adapting image vs. neutral control) and hemisphere (right vs. midline vs. left). The first analysis focused on a time window 400–800 ms, which has produced emotional effects in other studies over central parietal areas (Ashley et al., 2004; Huang and Luo, 2006; Schupp et al., 2004b, 2013; Weinberg and Hajcak, 2010). We found no effect of emotional afterimage within this time window at frontal sites [$F(2,42)=2.25$, $p=.12$] or central parietal sites [$F(2,42)=.29$, $p=.74$].

However, the same analysis over the frontal sites within an earlier time window (200–500 ms) produced a main effect of emotional afterimage [$F(2,42)=4.11$, $p<.05$, partial $\eta^2=.16$]; post hoc pairwise comparisons for this mid-latency frontal component adjusted for multiple comparisons (least significant differences) confirmed that sad afterimages produced a more positive amplitude than happy afterimages ($p=.025$) or neutral control trials ($p=.027$) whereas there was no difference in the amplitude for happy afterimages compared to neutral control trials (see Fig. 3). Although our component was observed more frontally, this observation is consistent with the pattern of results observed by others over central and parietal sites, at which negative emotional stimuli elicited a more positive LPC (Huang and Luo, 2006) or LPP (Ito and Cacioppo, 2000) response compared to positive emotional stimuli.

The main effect of hemisphere was also significant at the mid-latency frontal component [$F(2,42)=7.89$, $p<.01$, partial $\eta^2=.27$]; post hoc pairwise comparisons adjusted for multiple comparisons (least significant differences) confirmed that amplitude was smaller over the right hemisphere compared to left hemisphere ($p=.003$) and midline ($p=.008$) sites; left hemisphere and midline amplitudes did not differ. The interaction between hemisphere and emotional afterimage was not significant.

4. Discussion

Differential brain responses to positive and negative facial expressions are evident as early as the N170 ERP component (Batty and Taylor, 2003); however, it is not clear from previous research using emotionally expressive faces whether this difference reflects low-level effects of differences in the stimulus features, or whether there is a contribution from differences in perception of emotion. In the current study we compared responses to neutral faces with the same stimulus features but different perceived emotions. We observed a measureable difference in the N170 when observers *perceived* a neutral face as happy or sad, thus ruling out any low-level effects of the stimulus.

4.1. *The emotional afterimage*

The current study replicates previous behavioural results in the afterimage literature. When observers fixated a happy face, the neutral face that was briefly presented was likely to be labelled sad, whereas after fixating a sad face the same neutral face was likely to be labelled happy. In the control condition where participants fixated on a neutral expression, there was not a significant difference between happy and sad responses, indicating that participants did not perceive an emotion aftereffect in this condition. This is consistent with past work that has shown: (1) emotional facial expressions elicit aftereffects (Butler et al., 2008; Fox and Barton, 2007; Rutherford et al., 2008) and (2) each aftereffect is the psychological opposite (e.g. as red is to green in colour adaptation or happy is to sad in emotion adaptation) of the fixated stimuli. For example, Rutherford et al. (2008) found that when an observer fixated a happy face, a subsequently viewed neutral face was perceived as the psychological opposite: sad. When any negative expression was fixated, the subsequently viewed neutral face was seen as happy (Rutherford et al., 2008). In other words, there is a functional psychological organization of perceived emotions that allows functionally distinct emotions to be discriminated, presumably in order to adaptively inform behaviour. With respect to neural models of emotional processing, this functional psychological organization of perceived emotion may be

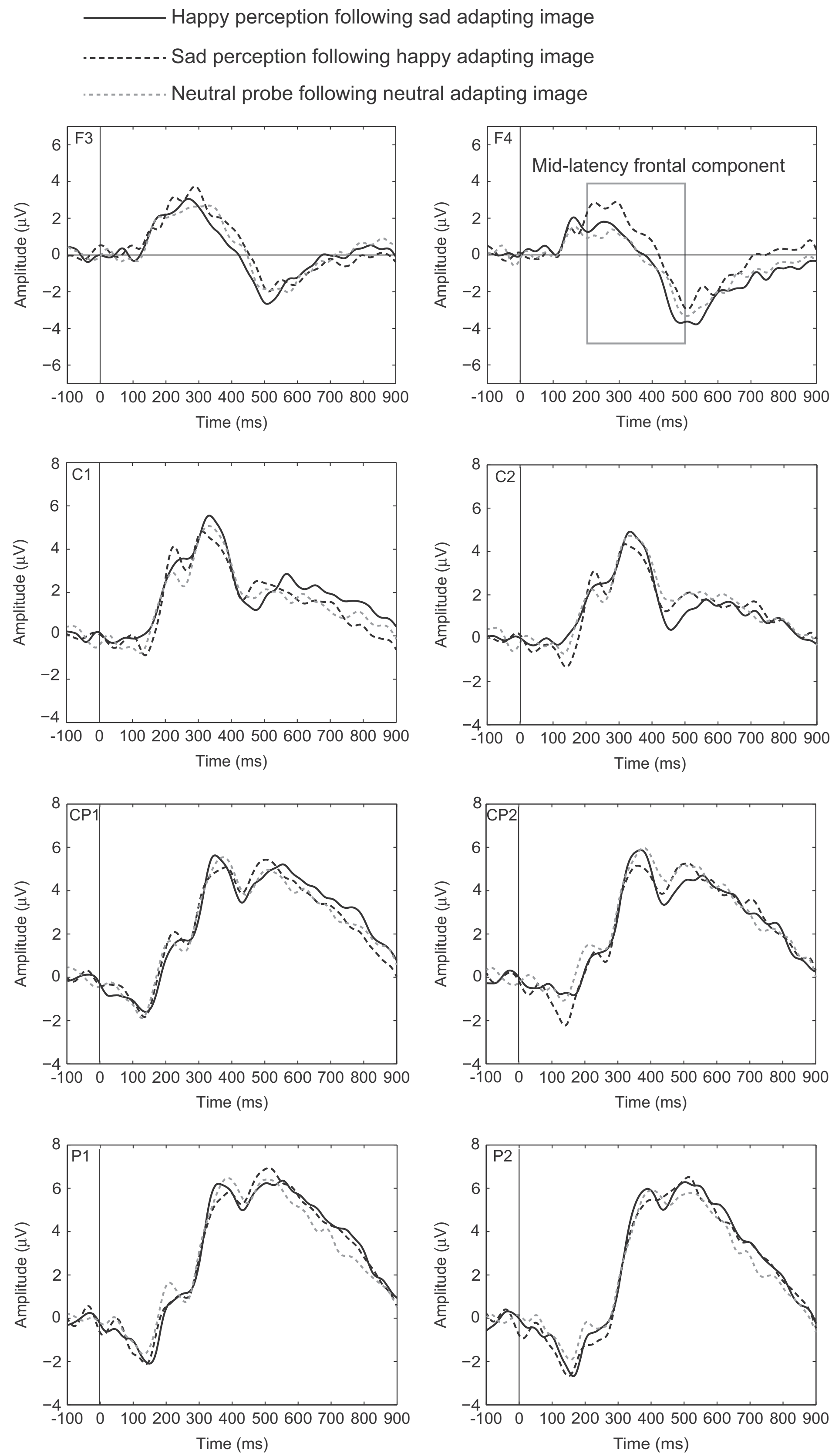

Fig. 3 – Event-related potential waveforms for parietal (P1, P2), central (CP1, CP2, C1, C1), and frontal (F3, F4) sites, in response to neutral probes following happy, sad, or neutral adapting images. Waveforms consist of averages for which the behavioral adaptation effect occurred (neutral probes were perceived as happy following sad adapting images or neutral probes were perceived as sad following happy adapting images). Neutral adapting images represent the control condition in which a neutral face was primed by the mirrored-image of the same neutral face; averages include both happy and sad responses. We applied a lowpass filter of 20 Hz to the grand averaged waveforms for visualization purpose only.

mediated by the fast and crude processing of the amygdala (Vuilleumier, 2005).

The nature of the task was a forced-choice paradigm in which no neutral option was available to the participant. One might speculate that this forced choice artificially created the observed behavioural results, but if there were no perceptual effect, one would expect participants to perceive the true neutral probe image as neutral, yielding responses that were statistically indistinguishable from 50% "happy" and 50% "sad". Furthermore, the ERP results support the observers′ emotion labels, providing corroborating evidence that the neutral face was perceived as happy or sad depending on the emotion of the preceding adapting stimulus.

4.2. *Neural processing of emotional perception*

Significant differences in the response of the N170 to the neutral probe faces depended on the adapting condition. The latency of the N170 component differentiated neutral faces based on the perception of happy versus sad facial expressions induced by emotion aftereffects. When participants perceived a neutral probe as happy (after adapting to a sad facial image) the response of the N170 peaked earlier compared to trials in which they perceived a neutral probe as sad (after adapting to a happy facial image). This pattern of results is consistent with previous studies that used true happy and sad images; Batty and Taylor (2003) reported an earlier peak latency of the N170 component for happy faces compared to sad faces, with no measurable differences in N170 amplitude. Thus, the current results make an important contribution by demonstrating that this N170 latency difference is associated with the perception of emotional facial expressions rather than purely stimulus-driven effects.

These results shed light on the question of whether the N170 is cognitively penetrable; in other words, whether there are any effects of expectations, prior knowledge, or experience on the response characteristics of the N170 (Heisz and Shedden, 2009; Jemel et al., 2003; Bentin and Golland, 2002). To date, evidence suggests that this early marker of face processing is cognitively penetrable. For example, Bentin and Golland (2002) presented scrambled schematic faces that were degraded to the point that they appeared to be unrelated objects in a circle. When a block of intact schematic faces preceded the scrambled schematic faces, the scrambled schematic faces elicited a larger N170, comparable to that elicited by intact faces. This result reflects a priming effect in which the scrambled schematic faces were seen as actual faces, and thus elicited a face-like N170 (Bentin and Golland, 2002). There is also evidence of differences in the N170 response depending on whether an impoverished two-tone Mooney face is familiar or not, highlighting the impact of prior knowledge on current perceptual processing (Jemel et al., 2003). Furthermore, evidence suggests that compared to novel faces, repeatedly presented faces elicit a smaller and earlier N170 response (Itier and Taylor, 2002; Heisz et al., 2006), demonstrating the effects of previous experience on current processing. The current study offers a different approach to this question, and supports the idea that the N170 is cognitively penetrable by showing that the latency of the N170 was affected by the perception of the neutral probe face as happy or sad.

We speculate that emotion aftereffects may reflect feedback input from other brain regions involved in early stages of emotion processing. Current neural models on the perception of emotion propose that emotional information is processed in two distinct but interactive ways (Morris et al., 1998; Vuilleumier, 2005). First, emotional information is rapidly fed forward for crude processing of emotional salience by the amygdala. Via re-entrant connections, this information is then fed-back into visual cortex and has the potential to modify perception. At the same time but at a much slower rate, the visual cortex is recruited for more detailed emotional processing of the stimulus that is needed for categorization and identification. The fast amygdala mediated emotional processes and the slower visually mediated emotional processes are believed to operate in parallel but interactive processing streams. This may be one mechanism by which the N170 is cognitive penetrable: facial affect may be processed quickly by the amygdala and then fed-back to early perceptual processing regions of the occipitotemporal area to modify the N170 response (Haxby et al., 2000; Johnson, 2013). This re-entry of emotional information from other brain regions may be driving the emotional aftereffects and the differences we observed in the N170 for our stimuli. While our experiment was not designed to address the contribution of re-entrant pathways, it is nonetheless interesting to consider the origins of this effect. Additional research is needed to evaluate the fit of these models.

Like previous research, we found that the N170 is slightly later when processing a negative emotion compared to a positive emotion. Although this temporal relationship seems counter-intuitive, Batty and Taylor (2003) offer a couple of plausible explanations. Perhaps negative emotions take longer to process because they include information processed via a subcortical pathway, thus accounting for the increase in response time (Batty and Taylor, 2003, p. 617). Alternatively, negative emotions may require attention that positive emotions do not (Schupp et al., 2004a; Weinberg and Hajcak, 2010), so the recruitment of attention may account for the increase in response time (Batty and Taylor, 2003, p. 618).

Our observations contrast with other reports that show larger EPN and LPP amplitudes to affective (positive and negative) stimuli compared to neutral stimuli, but do not show differential responses to positive vs. negative valence (Schupp et al., 2004b, 2013). We did not detect amplitude differences at EPN or LPP, which may reflect the processing differences between the more data-driven source of emotional content of the stimulus itself compared to the more perceptual source of the emotional content in the afterimages. However, we did observe modulation of a mid-latency frontal component, which was larger in amplitude when participants perceived a sad afterimage compared to when they perceived a happy afterimage or viewed a neutral control image. Although our observation was more frontal in topography compared to the LPP, the pattern is similar to other studies showing larger LPC or LPP responses to negative stimuli (Huang and Luo, 2006; Ito and Cacioppo, 2000; Weinberg and Hajcak, 2010). This effect is consistent with a negativity bias, in which negative emotional information holds a privileged status, leading to stronger responses (Cacioppo and Gardner, 1999; Huang and Luo, 2006). Both the delayed N170 and larger frontal positivity for sad afterimages support the idea that the perception of negative content requires additional cognitive resources. However, recent work claims that increases in the amplitude of the LPP reflect attentional effects to motivationally salient stimuli rather than negative stimuli, per se (Cuthbert et al., 2000; Weinberg and Hajcak, 2010); it is possible that motivational salience (rather than negative emotion) is driving the response in the perception of the sad afterimages in our study. The important finding of the current study is that the observed sensitivity to emotional valence is dependent on the perceived emotional content, not the physical emotional content.

The afterimage paradigm is generally interpreted as resulting from an opponent process in the visual system: happy is the psychological opposite of sad, and vice versa (Rutherford et al., 2008). In this view, one would predict that neural responses to both happy and sad faces would differ from neutral, and would differ in opposite directions. Indeed, we found responses on both happy adaptation and sad adaptation trials be significantly different from the neutral adaptation trials, and Fig. 1 clearly shows a significant stepwise progression of proportion of sad responses following fixation on sad, compared to neutral, compared to happy faces. However, this is not what we see in pattern of the N170 latency differences. While, happy afterimages peaked significantly earlier than sad afterimages, as predicted, the differences in latency between each emotional trial type and the latency on neutral adaptation trials were not statistically significant. That said, we cannot rule out the possibility that fixating the sad face and fixating the happy face both had effects on participants' neural responses. Similarly, the display showing relative N170 latencies in Fig. 4 is consistent with the possibility that the N170 latency following fixation of the neutral face is intermediate between the latencies following fixation of sad and happy faces, although this relationship did not reach statistical significance in the current study. Future research may provide a stronger test of the opponent coding hypothesis.

A limitation of the current study is the relatively low number of trials compared to what is traditionally included in ERP analyses. The aftereffect paradigm requires a relatively long presentation of the adapting face image. To accommodate this long exposure time in our experimental session, we included fewer trials in each condition. It is possible that differences at the EPN and/or the LPP components may be revealed in future experiments with increased number of trials. The emotional aftereffect paradigm also departs from the typical protocol used in ERP experiments such that the ISI between the adapting stimulus and the probe stimulus is zero. Our zero ISI did not provide a strong enough visual onset cue to trigger reliable early visual evoked potentials (e.g. P1). It is possible that this resulted in a delayed onset of the N170, however, the topographical voltage plot shows the typical N170 spatial distribution (Fig. 2), and allows us to confidently interpret our results as involving the face-relevant N170. This is the first study to examine neural responses to emotional aftereffects, combining the traditional emotional aftereffect behavioural paradigm with EEG measures. Future studies can further advance understanding of the neural activity associated with emotional aftereffects by exploring shorter adaptation durations, a greater number of trials, and longer ISI.

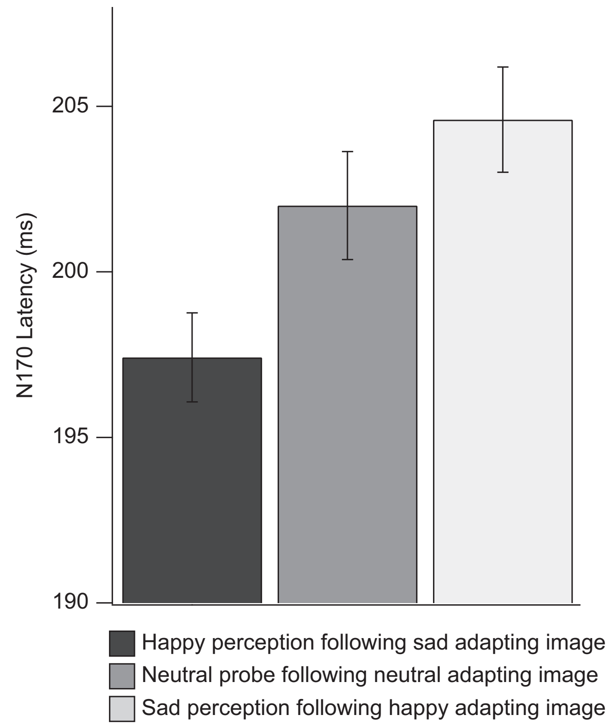

Fig. 4 – Mean (corrected standard error) N170 peak latency for emotional afterimages averaged across electrodes P7/P8 and PO7/PO8. Waveforms consist of averages for which the behavioral adaptation effect occurred (neutral probes were perceived as happy following sad adapting images or neutral probes were perceived as sad following happy adapting images). Neutral control condition averages include both happy and sad responses.

Taken together, the behavioural and ERP results of the current study suggest that the emotional aftereffects paradigm influences perceptual processing of neutral faces. First, the current results replicate the behavioural aftereffects phenomenon with respect to emotional facial expressions showing that a neutral face appears sad after the fixation of a happy face but happy after the fixation of a sad face. Further, ERP results show that the perceived emotion of a physically neutral stimulus affects the latency of the N170. In other words, the N170 is influenced by psychological representations independent of the physical stimulus.

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REFERENCES

Ashley, V., Vuilleumier, P., Swick, D., 2004. Time course and specificity of event-related potentials to emotional expressions. Neuroreport 15, 211.

Balconi, M., Pozzoli, U., 2003. Face-selective processing and the effect of pleasant and unpleasant emotional expressions on ERP correlates. Int. J. Psychophysiol. 49, 67–74.
Batty, M., Taylor, M.J., 2003. Early processing of the six basic facial emotion expressions. Cogn. Brain Res. 17, 613–620.
Bentin, S., Golland, Y., 2002. Meaningful processing of meaningless stimuli: the influence of perceptual experience on early visual processing of faces. Cognition 86, B1–B14.
Bentin, S., McCarthy, G., Perez, E., Puce, A., Allison, T., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8, 551–565.
Benton, C.P., Burgess, E.C., 2008. The direction of measured face aftereffects. J. Vision 8, 1–6.
Botzel, K., Schulze, S., Stodieck, S.R.G., 1995. Scalp topography and analysis of intracranial sources of face-evoked potentials. Exp. Brain Res. 104, 135–143.
Butler, A., Oruc, I., Fox, C., Barton, J., 2008. Factors contributing to the adaptation aftereffects of facial expression. Brain Res. 1191, 116–126.
Cacioppo, J.T., Gardner, W., 1999. Emotion. Annu. Rev. Psychol. 50, 191–214.
Campbell, J., Burke, D., 2009. Evidence that identity-dependent and identity-independent neural populations are recruited in the perception of five basic emotional facial expressions. Vision Res. 49, 1532–1540.
Cuthbert, B., Schupp, H.T., Bradley, M., Birbaumer, N., Lang, P., 2000. Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. Biol. Psychol. 52, 95–111.
Davidenko, N., Winawer, J., Witthoft, N., 2006. Gender aftereffects in the perception of silhouetted face profiles. J. Vision 6, 1068.
Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. J. Neurosci. Methods 134, 9–21.
Ekman, P., Friesen, W.V., 1976. Pictures of Facial Affect. Consulting Psychologists Press, Palo Alto, CA.
Fox, C.J., Barton, J.J., 2007. What is adapted in face adaptation? The neural representations of expression in the human visual system. Brain Res. 1127, 80–89.
Hajcak, G., Olvet, D.M., 2008. The persistence of attention to emotion: brain potentials during and after picture presentation. Emotion 8, 250–255.
Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cogn. Sci. 4, 223–233.
Heisz, J.J., Shedden, J.M., 2009. Semantic learning modifies perceptual face processing. J. Cogn. Neurosci. 21, 1127–1134.
Heisz, J.J., Watter, S., Shedden, J.M., 2006. Progressive N170 habituation to unattended repeated faces. Vision Res. 46, 47–56.
Hsu, S., Young, A.W., 2004. Adaptation effects in facial expression recognition. Visual Cogn. 11, 871–899.
Huang, Y.X., Luo, Y.J., 2006. Temporal course of emotional negativity bias: an ERP study. Neurosci. Lett. 398, 91–96.
Itier, R.J., Taylor, M.J., 2002. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. NeuroImage 15, 353–372.
Itier, R.J., Taylor, M.J., 2004. N170 or N!? Spatiotemporal differences between object and face processing using ERPs. Cerebral Cortex 14, 132–142.
Ito, T.A., Cacioppo, J.T., 2000. Electrophysiological evidence of implicit and explicit categorization processes. J. Exp. Soc. Psychol. 36, 660–676.
Jaquet, E., Rhodes, G., 2008. Face aftereffects indicate dissociable, but not distinct, coding of male and female faces. J. Exp. Psychol. Hum. Percept. 34, 101–112.
Jaquet, E., Rhodes, G., Hayward, W.G., 2008. Race-contingent aftereffects suggest distinct perceptual norms for different race faces. Visual Cogn. 16, 734–753.
Jemel, B., Pisani, M., Calabria, M., Crommelinck, M., Bruyer, R., 2003. Is the N170 for faces cognitively penetrable? Evidence from repetition priming of Mooney faces of familiar and unfamiliar persons. Cogn. Brain Res. 17, 431–446.
Johnson, M.H., 2013. Subcortical face processing. Nat. Rev. Neurosci. 6, 766–774.
Johnston, V.S., Miller, D.R., Burleson, M.H., 1986. Mulitple P3s to emotional stimuli and their theoretical significance. Psychophysiology 23, 684–694.
Krolak-Salmon, P., Fischer, C., Vighetto, A., Mauguière, F., 2001. Processing of facial emotional expression: spatio-temporal data as assessed by scalp event-related potentials. Eur. J. Neurosci. 13, 987–994.
Leopold, D.A., Rhodes, G., Muller, K.-M., Jeffery, L., 2005. The dynamics of visual adaptation to faces. R. Soc. Biol. Sci. 272, 879–904.
Little, A.C., DeBruine, L.M., Jones, B.C., 2005. Sex-contingent face after-effects suggest distinct neural populations code male and female faces. Proc. R. Soc. Biol. Sci. 272, 2283–2287.
Little, A.C., DeBruine, L.M., Jones, B.C., Waitt, C., 2008. Category contingent aftereffects for faces of different races, ages and species. Cognition 106, 1537–1547.
Luo, W., Feng, W., He, W., Wang, N., Luo, Y., 2010. Three stages of facial expression processing: ERP study with rapid serial visual presentation. NeuroImage 49, 1857–1867.
Morris, J.S., Oehman, A., Dolan, R.J., 1998. Conscious and unconscious emotional learning in the human amygdala. Nature 393, 467–470.
Moser, J.S., Hajcak, G., Bukay, E., Simons, R.F., 2006. Intentional modulation of emotional responding to unpleasant pictures: an ERP study. Psychophysiology 43, 292–296.
Pell, P.J., Richards, A., 2011. Cross-emotion facial expression aftereffects. Vision Res. 51, 1889–1896.
Rhodes, G., Jeffery, L., Clifford, C.W.G., Leopold, D.A., 2007. The time course of higher-level face aftereffects. Vision Res. 47, 2291–2296.
Rhodes, G., Jeffery, L., Watson, T.L., Clifford, C.W.G., Nakayama, K., 2003. Fitting the mind to the world: face adaptation and attractiveness aftereffects. Psychol. Sci. 14, 558.
Rossion, B., Gauthier, I., Tarr, M.J., Despland, P., Bruyer, R., Linotte, S., et al., 2000. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. Neuroreport 11, 69–74.
Rossion, B., Jacques, C., 2008. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. NeuroImage 39, 1959–1979.
Rousselet, G.A., Mace, M.J.M., Fabre-Thorpe, M., 2004. Animal and human faces in natural scenes: how specific to human faces is the N170 ERP component?. J. Vision 4, 13–21.
Russell, J.A., Fehr, B., 1987. Relativity in the perception of emotion in facial expressions. J. Exp. Psychol. Gen. 116, 223–237.
Rutherford, M.D., Chattha, H.M., Krysko, K.M., 2008. The use of aftereffects in the study of relationships among emotion categories. J. Exp. Psychol. Hum. Percept. 34, 27–40.
Rutherford, M.D., Troubridge, E., Walsh, J., 2012. Visual afterimages of emotional faces in high functioning autism. J. Autism Dev. Disord. 42, 221–229.
Schupp, H.T., Cuthbert, B., Bradley, M., Hillman, C., Hamm, A.O., Lang, P., 2004a. Brain processes in emotional perception: motivated attention. Cogn. Emot. 18, 593–611.
Schupp, H.T., Junghöfer, M., Weike, A.I., Hamm, A.O., 2003. Attention and emotion: an ERP analysis of facilitated emotional stimulus processing. Neuroreport 14, 1107–1110.

Schupp, H.T., Junghöfer, M., Weike, A.I., Hamm, A.O., 2004b. The selective processing of briefly presented affective pictures: an ERP analysis. Psychophysiology 41, 441–449.

Schupp, H.T., Schmälzle, R., Flaisch, T., Weike, A.I., Hamm, A.O., 2013. Affective picture processing as a function of preceding picture valence: an ERP analysis. Biol. Psychol. 92, 520–525.

Skinner, A.L., Benton, C.P., 2010. Anti-expression aftereffects reveal prototype-referenced coding of facial expressions. Psychol. Sci. 21, 1248–1253.

Vida, M., Mondloch, C.J., 2009. Children's representations of facial expression and identity: identity-contingent expression aftereffects. J. Exp. Child. Psychol. 104, 326–345.

Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. Trends Cogn. Sci. 9, 585–594.

Watson, T.L., Clifford, C.W.G., 2003. Pulling faces: an investigation of the face-distortion aftereffect. Perception 32, 1109–1116.

Webster, M.A., MacLin, O.H., 1999. Figural aftereffects in the perception of faces. Psychon. Bull. Rev. 6, 647–653.

Webster, M.A., Mollon, J.D., 1991. Changes in colour appearance following post-receptoral adaptation. Nature 349, 235–238.

Wede, J., Francis, G., 2006. The time course of visual afterimages: data and theory. Perception 35, 1155–1170.

Weinberg, A., Hajcak, G., 2010. Beyond good and evil: the time-course of neural activity elicited by specific picture subtypes. Emotion 10, 767–782.