Biological Psychology 120 (2016) 69–80

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Electrophysiological evidence for attentional capture by irrelevant angry facial expressions

Nicolas Burra*, Caroline Barras, Sélim Yahia Coll, Dirk Kerzel

Faculté de Psychologie et des Sciences de l'Education, Université de Genève, Switzerland

ARTICLE INFO

Article history:
Received 6 January 2016
Received in revised form 12 August 2016
Accepted 23 August 2016
Available online 24 August 2016

Keywords:
N2pc
Attentional capture
Angry faces

ABSTRACT

Attention is believed to be biased toward threatening objects or faces. Therefore, we tested whether angry face stimuli would capture attention even when they are irrelevant to the task. Observers searched for a neutral face with a tilted nose. On some trials, the target was shown together with an irrelevant angry or happy face and we measured the N2pc (an electrophysiological marker of attentional selectivity) to the distractor expression. We found that angry distractors triggered an N2pc, whereas happy distractors did not. Follow-up experiments explored the reliability of the N2pc to angry distractors using upright or inverted angry faces, the eye or mouth region of angry faces and face-like stimuli. We conclude that a threatening expression has a high attentional priority due to its emotional content and captures attention despite being irrelevant for the task.

1. Introduction

Facial expressions, especially threatening faces, are important to our survival, and are assumed to be preferentially detected. From an evolutionary perspective, preferential detection of threatening stimuli is adaptively beneficial (Lang, Davis, & Öhman, 2000), because a threat detection system would allow the attentional system to uncover possible threats with minimal allocation of attention to the surrounding environment (LeDoux, 1996). Some models of early emotional and attentional processing have proposed that threatening stimuli are processed prior to the operation of selective attention, with a specialized "threat-detection system" (Öhman & Mineka, 2001). Thus, the threat-capture hypothesis predicts automatic attentional capture by threatening stimuli to facilitate further processing.

Preferential attentional selection of threatening stimuli like angry faces has been observed in visual search of facial expressions and has been called the anger superiority effect (Hansen & Hansen, 1988). When participants were required to detect the presence of an angry face among happy faces or the presence of a happy face among angry faces, it was observed that participants are faster to detect angry faces than happy faces. Interestingly, the anger superiority effect persists with schematic faces (Eastwood, Smilek, & Merikle, 2001; Fox et al., 2000; Hansen & Hansen, 1988; Öhman, Lundqvist, & Esteves, 2001; Sawada & Sato, 2015) that are easily recognizable and are created with lines representing eyebrows and mouth surrounded by a circle or an oval. Typically, they share the same attributes as real faces, i.e. furrowed brows and a compressed mouth (Darwin, 1872; Ekman & Friesen, 1976) and receive similar evaluations in terms of valence and intensity (Calvo & Nummenmaa, 2008; Coelho, Cloete, & Wallis, 2010).

However, the interpretation of the anger superiority effect is controversial. A number of studies suggested that attentional capture by angry faces does not result from preferential attentional selection of threatening expressions, but from salient perceptual features associated with angry faces that vary strongly as a function of stimulus set (i.e. Horstmann, 2007; Horstmann, Lipp, & Becker, 2012; Lipp, Price, & Tellegen, 2009; Savage, Becker, & Lipp, 2016; Savage & Lipp, 2015; Savage, Lipp, Craig, Becker, & Horstmann, 2013). In addition, intentions or working memory have also been established as partially driving the anger superiority effect because they promote an attentional set to threatening content (Hahn & Gronlund, 2007; Moriya, Koster, & De Raedt, 2014; Todd, Cunningham, Anderson, & Thompson, 2012; Vogt, De Houwer, Crombez, & Van Damme, 2013). Consequently, the advantage of angry faces might be the consequence of goal-driven attention more than involuntary attentional capture.

In fact, bottom-up attentional capture is typically observed in response to irrelevant, but highly salient stimuli that compete with task-relevant stimuli so that attention moves to the irrelevant distractor before it reaches the target (Theeuwes, 1992, 2010). At the

* Corresponding author at: Faculté de Psychologie et des Sciences de l'Education, Université de Genève, 40 bd du Pont d'Arve, Geneva, Switzerland.
E-mail address: nicolas.burra@unige.ch (N. Burra).

http://dx.doi.org/10.1016/j.biopsycho.2016.08.008

level of simple features, it has been established that color, shape, size, luminance and onsets may capture attention (Schreij, Owens, & Theeuwes, 2008). However, evidence for the involuntary capture of attention by complex features, like the human face and facial expressions, has been relatively scarce.

Some have addressed the threat-capture hypothesis by asking participants to search for a singleton target in competition with an irrelevant facial expression (Hodsoll, Viding, & Lavie, 2011; Huang, Chang, & Chen, 2011). Despite establishing that irrelevant facial expressions resulted in longer RTs, these experiments failed to establish a significant difference in paired comparisons between angry and happy distractors. However, it may be that behavioral measures (reaction times, RTs) are not sensitive enough to detect stronger attentional capture by angry faces compared to happy faces. In particular, the threat-capture hypothesis states that threatening expressions are detected early in the visual processing chain and lead to early attentional selection, but RTs are the result of a multitude of processing stages. Thus, differences in RTs may reflect early attentional selection or late response-related biases. Also, it may be that RTs increase because displays with an emotional distractor are visually more complex, which may lead to spatially unspecific filtering costs (Kahneman, Treisman, & Burkell, 1983). To ascertain that facial expressions result in early attentional capture (vs. late response-related biases), we measured an electrophysiological correlate of attention, the N2pc, which occurs only 200–300 ms after stimulus onset and indicates the attended hemifield, which makes it a spatially specific measure (vs. spatially unspecific filtering costs).

In general, attentional selectivity in visual search tasks has been investigated using lateralized event-related potentials (ERPs). The N2pc is a negative deflection in electrodes contralateral to the target at posterior sites in the N2 latency range, about 200–300 ms after stimulus onset (Eimer, 1996; Luck & Hillyard, 1994). Functionally, the N2pc component is usually associated with the attentional selection of task-relevant stimuli (Eimer, 1996) or with the inhibition of distractors (Luck & Hillyard, 1994). More recent studies suggest that the N2pc consists of two subcomponents, a target negativity (N_T) that reflects enhancement of relevant information and a distractor positivity (P_D) that reflects inhibition of distractors (e.g., Feldmann-Wüstefeld, Uengoer, & Schubö, 2015; Hickey, Di Lollo, & McDonald, 2009; Kiss, Grubert, Petersen, & Eimer, 2012; Sawaki & Luck, 2013). In addition, the N2pc component reflects involuntary attentional capture when the distractor is shown at a lateral position and the target is on the vertical midline, so that any lateralized component has to be ascribed to the distractor (Burra & Kerzel, 2013, 2014; Hickey, McDonald, & Theeuwes, 2006; Kiss et al., 2012). Furthermore, the sensitivity of the N2pc to attentional capture may be greater than the sensitivity of RTs (Ansorge, Horstmann, & Worschech, 2010; Eimer & Kiss, 2008; Huber-Huber, Grubert, Ansorge, & Eimer, 2015).

With respect to the detection of angry **target** faces, some studies report facilitated detection of angry target faces compared to happy faces using RTs and the N2pc, that is, a larger N2pc for angry than happy target faces (Feldmann-Wüstefeld, Schmidt-Daffy, & Schubö, 2011; Weymar, Löw, Öhman, & Hamm, 2011; Yao, Ding, Qi, & Yang, 2013, Yao, Ding, Qi, & Yang, 2014), but studies investigating the electrophysiological correlates of angry or happy **distractor** faces are missing. Attentional capture by threatening face distractors would support the initial assumption of preferential threat detection that operates independently of the observer's volition.

In the present research, we investigate attentional capture by an irrelevant distractor in visual search. That is, we used an array of neutral expressions and a single distractor expression (Eastwood et al., 2001). Participants were asked to indicate the orientation of a tilted bar (the nose) inside a neutral face in an array of six faces (see Fig. 1). The N2pc as a marker of attentional selectivity

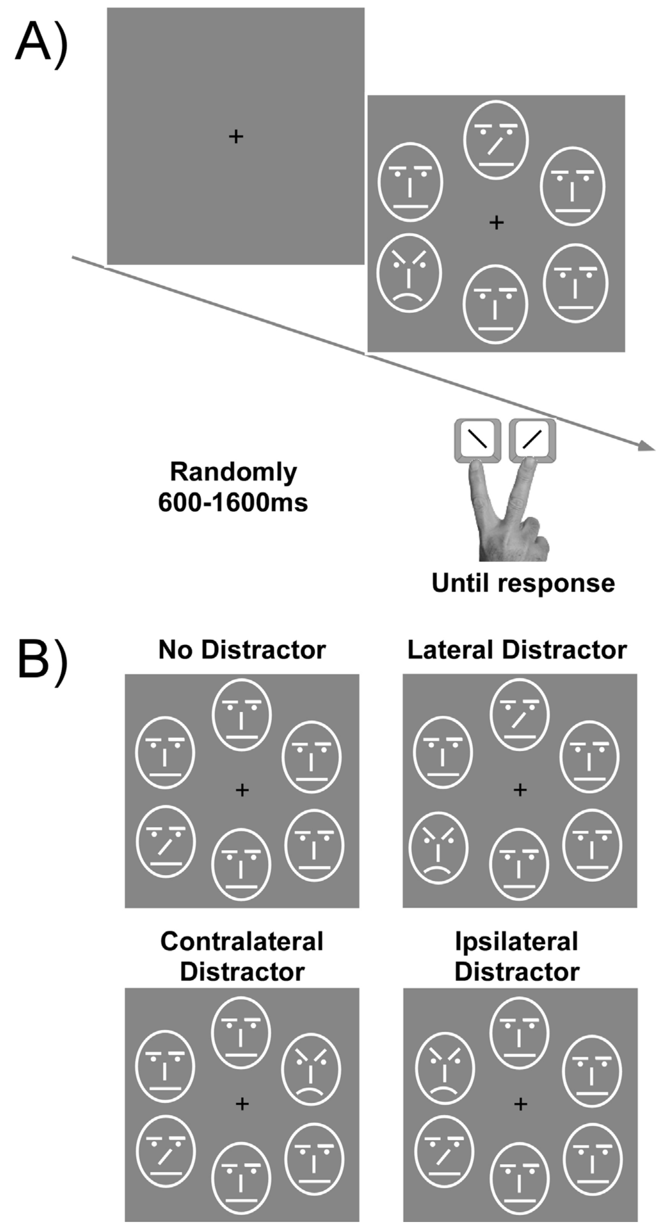

Fig. 1. Visual search task and spatial configurations. Six faces were presented on a virtual circle at 6° from the center. Panel A shows that participants had to press one of two buttons according to the orientation of the line representing the nose of the target. The spatial configurations in Experiment 1 are shown in panel B. In the no distractor condition, the target was on a lateral position and the distractor was absent (1/3 of trials). In the lateral distractor condition, the target was on the vertical midline and the distractor was on a lateral position (1/3 of trials). In the contralateral distractor condition, the target was on a lateral position and the distractor was on the opposite side (1/6 of trials). In the ipsilateral distractor condition, the target was lateral and the distractor was on the same side (1/6 of trials). The lateralized event-related potential was only analyzed for the lateral distractor condition.

(Burra & Kerzel, 2013, 2014; Hickey et al., 2006; Kiss et al., 2012) only picks up responses to lateralized stimuli. Therefore, we were particularly interested in a spatial configuration where the distractor was on a lateral position, whereas the target was on the vertical midline, above or below fixation. Importantly, this spatial configuration allows us to compare attentional capture by lateral positive (happy) and threatening (angry) distractor expressions. To control for low-level differences among our stimuli that might otherwise compromise lateralized ERPs, we used schematic faces. At the behavioral level, we expect a delay in RTs when comparing the distractor-present and distractor-absent conditions without any difference between facial expressions (Hodsoll et al., 2011; Huang et al., 2011).

2. Experiment 1a

2.1. Method

2.1.1. Participants

Twenty-one students of the University of Geneva (8 male) without any neurological or psychiatric indications participated in this experiment for class credit. Participants were naive as to the purpose of the experiment. The local ethics committee had approved the study and informed consent was obtained from participants prior to the experiment. The data of three participants were removed because less than 60% of the trials remained after artifact rejection. The data of two further participants were removed because of mean EOG traces outside the acceptable range (see below). Thus, the following analyses were conducted on the sixteen remaining participants (7 male).

2.1.2. Stimuli

We used the Cogent toolbox (www.vislab.ucl.ac.uk/Cogent2000) for Matlab to display the stimuli. Six stimuli were presented at 6° of eccentricity on a flat-panel screen. The gray used to draw the outlines had an approximate luminance of 11.6 cd/m^2 and the background was black. Luminance was measured with a ColorCAL MKII Colorimeter (Cambridge Research Systems) that was placed directly on a central rectangle filled with the same gray used for the outlines of the schematic faces. An oval of 1.8° horizontal by 2° vertical was shown as the contour of the faces. Inside each oval, a schematic face was created (see Fig. 1A) with two dots representing the eyes. Moreover, for the neutral faces, two horizontal bars were shown as eyebrows and a single horizontal bar as mouth. To create happy and angry facial expressions, the eyebrows were tilted at ± 40° from horizontal and a curved line, upright for happy and inverted for angry, replaced the horizontal line for the mouth. The size of the lines was scrupulously controlled to be equal among facial expressions, particularly for the mouth, in order to avoid any low-level confound. The target consisted of a bar, the nose, in the center of the face and tilted at ± 45° from vertical while the remaining noses consisted of a vertical bar. In 1/3 of the trials, no distractor expression was shown (see Fig. 1B). Consistent with our previous studies (Burra & Kerzel, 2013, 2014), the main condition to isolate the distractor-related N2pc was a display with the target on the vertical midline and the distractor on a lateral position (1/3 of trials), which elicited an N2pc to the distractor, but not to the target. To make target and distractor positions unpredictable, the distractor also occurred ipsilateral (1/6 of trials) and contralateral (1/6 of trials) to the target. As the latter conditions do not directly test our experimental hypothesis, they will not be analyzed any further. The distractor expression was randomly happy or angry. Furthermore, the schematic faces were validated by a group of 18 independent participants (see supplementary Figure A). Results were consistent with the valence and intensity of other picture sets (Öhman et al., 2001; Coelho et al., 2010; Weymar et al., 2011). Angry stimuli were rated as more negative and intense than happy stimuli.

2.1.3. Procedure

Condition order was randomized within blocks of 48 trials that took about 2 min to complete. Each trial began with a gray fixation cross on a black background for a random interval between 600 and 1600 ms. The stimulus remained on the screen until a response was given. Participants were asked to perform a 2-AFC task based on line orientation. They judged whether the only nose that was not vertical was tilted to the left or right. Participants were asked to respond as quickly as possible while maintaining accuracy above 90%. Responses were given with the right hand, using two keys of a standard keyboard. Incorrect responses were indicated by a message displayed at the center of the screen. Before the experiment, participants completed 48 trials of the task in which they were trained to avoid moving their eyes in direction of the target. Each participant performed 24 blocks of 48 experimental trials, each for a total of 1152 trials.

2.1.4. Electrophysiological recording and analysis

A Biosemi (Amsterdam, The Netherlands) ActiveTwo amplifier system AD-Box with 64 active AG/AgCL electrodes sampled at 1024 Hz was used. We used the voltage difference of two horizontal electro-oculogram (HEOG) electrodes, fixed at the outer canthi of the eyes, to detect horizontal and vertical eye movements. The two earlobes were used as online and offline References.

Data were filtered online with a 0.01 Hz high pass filter and a 100 Hz low-pass filter. Using BrainVision Analyzer 2.1 (Brain Products GmbH., Munich, Germany), we filtered the data with a zero-phase-shift, low-pass Butterworth filter (40 Hz with 24 dB/oct.). In order to remove ocular artifacts (blinks or saccades), we used independent component analysis. Trials corresponding to incorrect behavioral performance, trials with response time shorter than 200 ms and longer than 2000 ms were eliminated from the analysis. Then, a baseline correction (−100 ms to stimulus onset) was performed before the artifact exclusion. We excluded blinks (VEOG ± 60 μV), vertical or horizontal ocular movements (HEOG or VEOG ± 40 μV) and all other artifacts (all electrodes ± 100 μV). If in doubt about the signal, epochs were manually checked. Then, according to the procedure described by Luck (2005), in order to be sure that our participant did not move their eyes, we computed the average HEOG for left and right target conditions separately and rejected two subjects whose HEOG from 0 to 350 ms was larger than ± 3 μV. Thereby, participants did not move their eyes more than ~0.4° from the fixation point throughout the artifact free trials. On average, 18% of the trials were removed. The same procedure of artifact rejection was used in all of the following experiments.

Epochs started at 100 ms before the onset of the display and ended at 350 ms after, for a total time window of 450 ms. When necessary, we corrected for the non-sphericity of our data by using the Greenhouse-Geisser correction of the degrees of freedom. To maximize the amplitude of the N2pc and the differences between conditions, we measured the N2pc from 230 to 300 ms[1] at the P7/P8 electrodes, rather than at the most common PO7/PO8 electrodes.

Behavioral analyses were conducted on median RTs for each condition and participant. We compared distractor-absent and distractor-present trials across spatial configurations of target and distractor. The results did not differ significantly when we only analyzed RTs from distractor-present displays with the target at a midline position and the distractor at a lateral position. The same procedure of artifact rejection was used in all of the following experiments. The *t*-tests were always two-tailed.

2.2. Results

2.2.1. Behavior

A one-way repeated-measure ANOVA (distractor type: absent, happy, angry) revealed that RTs increased with happy (631 ms) and angry (633 ms) distractors compared to distractor absent trials (606 ms), $F(2,30) = 9.31$, $p < 0.001$, $\eta_p{}^2 = 0.39$. The two distractor

[1] This time window matches other studies using the additional singleton paradigm: 230–290 ms in Hickey et al. (2006); 200–280 ms in Burra and Kerzel (2013, 2014); 225–325 ms in McDonald et al. (2013); 220–300 ms in Kiss et al. (2012).

Table 1
Mean reaction times (in ms) and between-subject standard deviations (in parenthesis) from Experiments 1–4. There was either no distractor (absent), a happy, or an angry distractor expression. In Experiment 2, the faces were either upright or inverted and in Experiment 3, either the eyes or the mouth region was shown. In Experiment 4, face-like stimuli were used.

	Absent		Happy	Angry	
Exp. 1a	606 (71)		631 (78)	633 (81)	
Exp. 1b	676 (129)		728 (168)	754 (158)	
	Upright	Inverted		Upright	Inverted
Exp. 2	622 (89)	624 (100)		669 (112)	664 (119)
	Eyes	Mouth		Eyes	Mouth
Exp. 3	578 (47)	569 (47)		603 (48)	594 (50)
Exp. 4	592 (81)		613 (86)	621 (82)	

conditions were not significantly different ($p = 0.82$). We subjected proportion correct to the same ANOVA, but no significant effect was observed. Overall, the proportion of correct responses was 0.97 (see Table 1).

2.2.2. ERPs to lateralized distractors

Average contra- and ipsilateral ERPs to happy and angry distractors are shown in Fig. 2. A paired-samples t-test showed that the voltage difference to angry distractors (-0.62 μV) was significantly more negative than the voltage difference to happy distractors (0.18 μV), $t(15) = 3.72$, $p = 0.002$, $d = 0.92$. Moreover, one-sample t-tests against zero confirmed a significant N2pc to the angry distractor, $t(15) = 3.23$, $p = 0.006$, $d = 0.83$, but the lateralized ERP to happy distractors did not reach the level of significance, $p = 0.3$.

3. Experiment 1b

In Experiment 1a, we did not observe behavioral differences between angry and happy distractor faces while the N2pc components were different. Possibly, the difference between angry and happy was lost in processing stages succeeding the N2pc-interval. To isolate early processing stages, we masked the stimuli after 200 ms and measured RTs.

3.1. Methods

Twenty participants (4 male) participated. This experiment was similar to Experiment 1a except that the mouth, the eyes, and the eyebrows disappeared and were replaced by a mask 200 ms after the onset of the visual search display. The mask consisted of 250 dots that were spread inside the face contour without covering the nose. Mask and nose were displayed until a response was given. Thus, the central bars (i.e., the noses), including the response-relevant tilted nose, remained visible until a response was given, which made sure that the response requirements did not change with respect to Experiment 1a. There was a total of 192 trials.

3.2. Results

A one-way repeated-measure ANOVA (distractor type: absent, happy, angry) revealed that RTs increased with happy (728 ms) and angry (754 ms) distractors compared to distractor absent trials (676 ms), $F(2,38) = 23.96$, $p < 0.001$, $\eta_p^2 = 0.55$. Importantly, the two distractor conditions were significantly different, $t(19) = 2.36$, $p = 0.029$, $d = 0.56$. These behavioral effects are consistent with the electrophysiological evidence for attentional capture by angry, but not happy distractor expressions. The mask may have isolated early processing stages because the information about facial features was only available for 200 ms. Further, we subjected proportion correct to the same ANOVA, but no significant effect was observed. Overall, the proportion of correct responses was 0.97 (see Table 1).

3.3. Discussion

In Experiment 1a, we established behavioral interference from both angry and happy distractors. However, we observed an N2pc only to angry, but not to happy **distractor** expressions. Similarly, the N2pc to face **targets** was found to be larger for angry than happy expressions, suggesting a preferential selection of angry faces (Feldmann-Wüstefeld et al., 2011; Weymar et al., 2011; Yao et al., 2013). As in prior studies, Experiment 1a confirmed increased RTs for emotional expressions without significant differences between angry and happy faces (Hodsoll et al., 2011; Huang et al., 2011). However, when we reduced the presentation time by masking the facial features after 200 ms in Experiment 1b, we observed stronger interference from angry than happy distractors. Thus, processes occurring after 200 ms may obscure the initial difference between angry and happy distractors that is visible in the ERPs. We have no precise idea of what these processes may be, but we suspect that response selection and top-down scanning strategies may play a role.

Thus, we have demonstrated that a task-irrelevant angry distractor produced electrophysiological evidence for attentional capture. That is, when searching for a tilted bar inside a neutral face, only angry faces resulted in an N2pc. Interestingly, the N2pc toward the irrelevant facial distractor was different between angry and happy expressions despite the similar RTs. In sum, ERPs reflect involuntary attentional selection of threatening but not happy distractor expressions despite equal RTs when faces were shown until response.

Unfortunately, the anger superiority effect may be affected by a perceptual confound (Horstmann, 2007). According to this account, facilitated detection of angry faces might be strongly associated with the interaction of internal facial features (i.e. the mouth and eyebrows) and the contour of the face. Particularly, angry expressions may be preferentially detected due to closure (eyebrows and upper outline of the face, mouth and lower outline of the face). In order to rule out this possibility, we ran three additional experiments. In Experiment 2, we investigated the effect of presenting the angry face upside-down. In Experiment 3, we examined the role of internal facial features (eye/mouth) of the angry distractor expression in the capture effect. Finally, in Experiment 4, we quantified the impact of pure saliency-driven capture by using face-like stimuli that share features with facial expressions (Coelho et al., 2010). We predict that the N2pc will be present and significantly larger for upright than inverted angry expressions and for the eye than the mouth region. Finally, we expect the difference between angry and happy facial expressions to be absent for face-like stimuli.

4. Experiment 2

The face literature suggests that faces are processed holistically. Thus, they are perceived and characterized as a whole, rather than based on the sum of the individual features (Tanaka & Farah, 1993). In recognition of facial expressions, features are important (Tanaka,

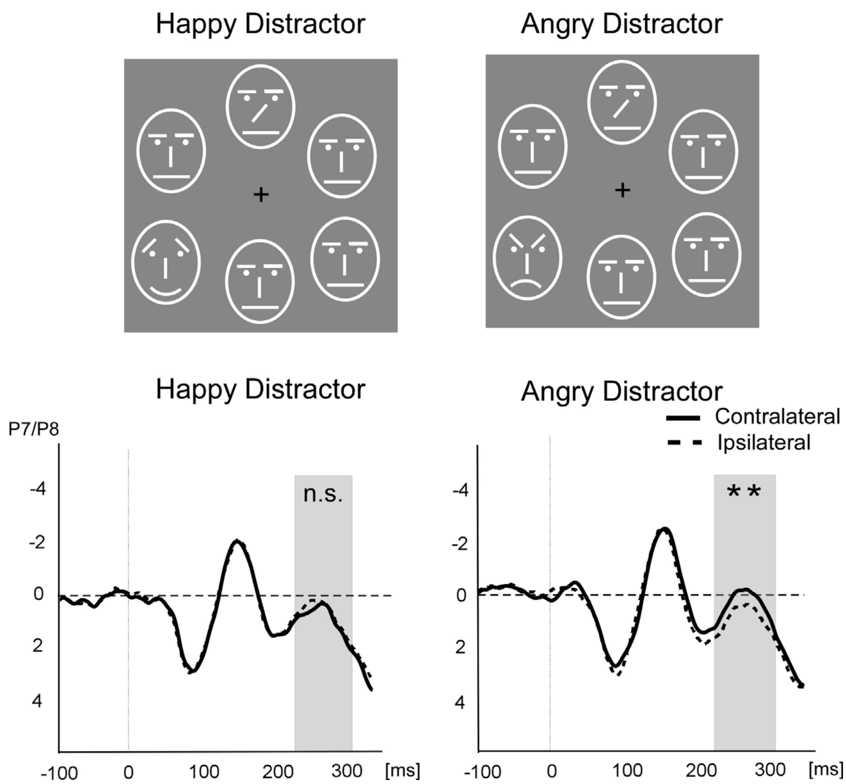

Fig. 2. Top: Sample displays from Experiment 1. Bottom: Results from Experiment 1. We evaluated the N2pc in the interval from 230 to 290 ms. Note: $^{**} = p < 0.01$ and n.s. = not significant.

Kaiser, Butler, & Le Grand, 2012), but holistic processing permits integration of facial features into a meaningful coherent representation of a facial expression (Calder & Jansen, 2005; Calder, Young, Keane, & Dean, 2000).

Moreover, holistic processing is central to the emergence of the anger superiority effect. Consequently, the anger superiority effect does not occur in visual search with upside-down faces (Fox et al., 2000; but see Öhman et al., 2001 for other results). In fact, inversion of faces disrupts the integration of configural relationships among facial features (Farah, Tanaka, & Drain, 1995; Tanaka & Sengco, 1997; Valentine, 1988; Yin, 1969), but at the same time, inversion allows keeping the individual perceptual features unchanged.

Using the inversion effect to our benefit, we presented only angry distractor expressions that were either upright or upside-down. Thus, inversion enables us to rule out that the N2pc toward the angry distractor expression is related to low-level perceptual confounds, like a preferential detection of tilted bars that are present in the eyebrows of both happy and angry expression, but which might be more perceptible in angry expressions. If low-level accounts were true, we should obtain an N2pc to the angry distractor of the same amplitude in upright and inverted orientations. If the N2pc occurred only to the upright angry distractor, this would show that attentional capture was related to the holistic processing of angry faces and their emotional content.

4.1. Method

4.1.1. Participants

Twenty-three new participants (10 male) from the same pool as above took part. The data of five participants were removed because less than 60% of the trials remained after artifact rejection. The data from one further participant was removed because the mean EOG traces were outside the acceptable range, leaving seventeen participants (8 male) in the final sample.

4.1.2. Stimuli

The present experiment was similar to Experiment 1a except for the distractors. Only the angry face was kept and it was presented in an upright or inverted condition.

4.1.3. Procedure

The procedure was similar to Experiment 1a. However, in half of the trials (512 trials) the stimuli were upright and in the other half, inverted. Their appearance was randomly mixed.

4.1.4. EEG recording and analysis

Using the same criteria as in Experiment 1a, 29% of the trials were removed.

4.2. Results

4.2.1. Behavior

A 2 (distractor: absence, presence) x 2 (face orientation: upright, inverted) repeated-measure ANOVA revealed that the presence of a distractor increased RTs (623 vs. 667 ms), $F(1,16) = 33.58$, $p < 0.001$, $\eta_p^2 = 0.21$. Inversion had no effect ($p = 0.779$), but the interaction approached significance, $F(1,16) = 4.25$, $p = 0.056$, $\eta_p^2 = 0.21$, showing that the distractor effect was slightly stronger in upright (47 ms) than in inverted orientation (40 ms). The analysis of proportion correct did not yield any significant results. Overall, the proportion of correct responses was 0.97 (see Table 1).

4.2.2. ERPs to lateralized distractors

Average contra- and ipsilateral ERPs to inverted and upright distractors are shown in Fig. 3. A paired-samples t-test revealed a larger N2pc for upright (-0.38 µV) than inverted threatening distractors (0.17 µV), $t(16) = 2.63$, $p = 0.018$, $d = 0.66$. One-sample t-tests showed that the N2pc to the lateral angry distractor was

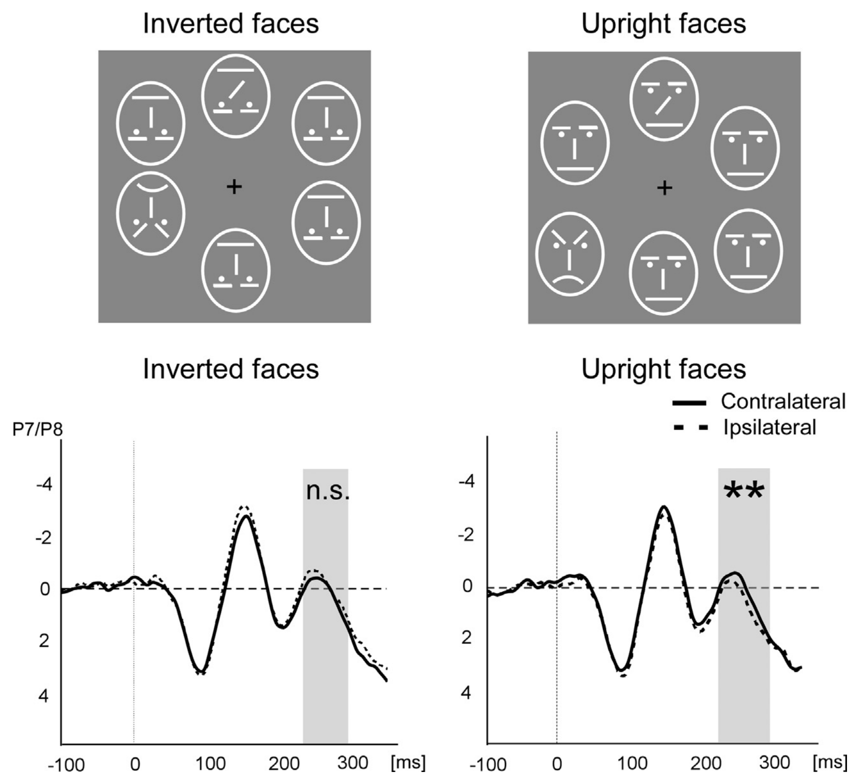

Fig. 3. Top: Sample displays from Experiment 2 with inverted faces. Bottom: Results from Experiment 2. Note: ** = $p < 0.01$ and n.s. = not significant.

significant when the face was upright, $t(16) = 3.31$, $p = 0.004$, $d = 0.80$, but not when it was inverted, $p = 0.351$.

4.3. Discussion

The results confirmed an N2pc to an angry distractor expression when it was upright, but not when it was inverted. Thus, attentional capture by an angry distractor cannot be due to better detection of oblique lines in schematic angry eyebrows, because these lines are similar in upright and inverted orientations. We think that the holistic processing of faces, which typically facilitates the accurate recognition of facial expressions, precedes attentional capture by upright faces. Consequently, the attentional priority of the threatening stimulus after recognition and appreciation of its emotional content is likely to explain attentional capture.

5. Experiment 3

Another possible confound is the "closure" feature (Wolfe & Horowitz, 2004) caused by the angry mouth neighboring the lower edge of the schematic face, which may pop out in visual search (Elder & Zucker, 1993, 1994; Wolfe & Horowitz, 2004). This feature is part of an angry expression, but not present in neutral or happy faces. Thus, during visual search for an angry target expression, the presence of closure may confer both speed and efficiency advantages (Mak-Fan, Thompson, & Green, 2011). While this effect has not been investigated with angry faces as distractors, one may argue that closure explains the capture by angry distractors. To isolate the closure feature, we split our stimuli into mouth and eye region, but kept the outline of the face. If closure explains the N2pc toward angry face distractors, an N2pc is expected to the mouth region, but not to the eye region.

Moreover, this manipulation allowed us to test whether the eye region has a larger importance than the mouth region. It has been claimed that the upper part of the face is more important than the lower part, due to the presence of the eyes (Haxby, Hoffman, & Gobbini, 2000; Schyns, Bonnar, & Gosselin, 2002; Schyns & Oliva, 1999) and preferentially triggers shifts of attention compared to the lower part of the face, especially for threatening faces (Fox et al., 2000; Tipples, Atkinson, & Young, 2002). Moreover, the greater importance of the upper features of the face relative to the lower features has been demonstrated in recognition of facial expressions (Baron-Cohen, 1997). The eyes seem to be crucial for recognizing angry or fearful faces but less so for happy faces (Bombari et al., 2013; Fox et al., 2000; Schyns, Petro, & Smith, 2007; Tanaka et al., 2012). In sum, if the eye region was sufficient to capture attention, we should obtain an N2pc to the eye region, but not to the mouth region.

5.1. Method

5.1.1. Participants

Twenty students of the University of Geneva (8 male) participated. The data from three participants were removed because less than 60% of the trials remained after artifact rejection. The data from one further participant were removed because of mean EOGs outside the acceptable range, leaving sixteen participants (6 male) for analysis.

5.1.2. Stimuli

The experiment was similar to Experiment 1a with the following exceptions. We divided the faces in mouth region (lower part) and eye region (upper part). Only angry faces were used.

5.1.3. Procedure

The procedure was similar to Experiment 1a. Mouth and eye displays were randomly mixed.

5.1.4. EEG recording and analysis

We used the same settings as in Experiment 1a. On average, 16% of the trials were removed.

5.2. Results

5.2.1. Behavior

A 2 (distractor: absence, presence) x 2 (face region: eye, mouth) ANOVA revealed that the presence of a distractor increased RTs (573 vs. 599 ms), $F(1,15) = 63.44$, $p < 0.001$, $\eta_p^2 = 0.80$. The distractor effect was similar for both face regions, as evident in the non-significant interaction, $p = 0.96$. No significant effects were observed in the analysis of proportion correct. Overall, proportion correct was 0.97 (see Table 1).

5.2.2. ERPs to lateralized distractors

Average contra- and ipsilateral ERPs to the mouth and eye region of angry distractors are shown in Fig. 4. A paired-samples *t*-tests showed that the N2pc was more negative to lateral distractors showing the eye region (-0.40 μV) than to lateral distractors showing the mouth region (0.19 μV), $t(15) = 2.26$, $p = 0.039$, $d = 0.57$. One-sample *t*-tests against zero revealed a significant N2pc for the eye region, $t(15) = 2.32$, $p = 0.035$, $d = 0.58$, but not for the mouth region, $p = 0.37$.

5.3. Discussion

This experiment establishes an N2pc to the eye region of irrelevant angry faces, but not to the mouth region, ruling out the possibility that the N2pc to angry distractor expressions was driven by the mouth region, which may be reduced to the low-level effect of closure. Moreover, the results are in line with previous research showing that the eye region contains the elements of a threatening face that capture attention (Fox & Damjanovic, 2006). It is likely that a "face" contour might enhance holistic processing and might lead to a filling-in effect (Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002; Righart, Burra, & Vuilleumier, 2011), so that the eye region in isolation might be sufficient to result in the perception of a whole schematic face, whereas the mouth region is insufficient. However, when the contour of the face is removed, the N2pc to angry eyes or eyebrows in isolation does not reach the level of significance (Weymar et al., 2011; Experiment 2 and 3), underlining the importance of the face outline and the face context in the anger superiority effect (Schubö, Gendolla, Meinecke, & Abele, 2006). Thus, our data support the idea that the eye region is preferentially processed in the perception of angry faces (Schyns et al., 2007; Vinette, Gosselin, & Schyns, 2004) and might therefore drive attentional capture to angry faces.

6. Experiment 4

Finally, even if schematic faces reduce the likelihood of low-level confounds, different studies have established that they do not completely rule them out (Horstmann & Bauland, 2006; Purcell & Stewart, 2010). Besides the closure effect, lines crossing the face outline have been suggested as a possible explanation for the anger superiority effect. Indeed, when the face outline is removed or manipulated in the display, the anger superiority effect disappears (Horstmann & Bauland, 2006; Schubö et al., 2006). Furthermore, it has been demonstrated that even meaningless face-like stimuli can generate an anger superiority effect (Coelho et al., 2010). In the same vein, geometrical shapes, such as inverted triangles, might be seen as emotional (Larson, Aronoff, & Stearns, 2007; Watson, Blagrove, & Selwood, 2011) and were found to activate the amygdala (Larson, Aronoff, Sarinopoulos, & Zhu, 2009) and increase peripheral physiological responses (Armbruster, Suchert, Gärtner, & Strobel, 2014), which has been linked to affective processing. Consequently, we wondered whether geometrical shapes would produce a capture effect similar to the one we observed for angry faces.

Therefore, we replicated the procedure of Experiment 1a, but used face-like stimuli similar to Coelho et al. (2010). If low-level features explain the N2pc toward threatening distractors, a larger N2pc to face-like threatening than to face-like happy stimuli is expected. If only the emotional content of angry faces explains the attentional capture by angry distractor faces, the N2pc to face-like threatening and face-like happy stimuli is not expected to differ.

6.1. Participants

Seventeen students of the University of Geneva (6 male) participated. Data of one female participant was rejected because less than 60% of the trials remained after artifact rejection, leaving sixteen participants in the final analyses.

6.2. Stimuli

We used shapes sharing internal features with faces, but which were not faces (Coelho et al., 2010). These stimuli were created by replacing the mouth by inverted eyebrows. In addition to the two pairs of eyebrows, the nose was shown (see Fig. 5).

6.3. Procedure

The procedure was similar to Experiment 1a. We avoided contextual effects by not speaking about faces. Thereby, participants would not be encouraged to see these stimuli as faces. As in the preceding experiments, participants were required to search for the tilted bar.

6.4. EEG recording and analysis

We used the same settings and statistics as in Experiment 1a. On average, 13% of the trials were removed from the EEG data.

6.5. Results

6.5.1. Behavior

A one-way repeated-measures ANOVA (distractor type: absent, face-like happy, face-like angry) revealed that the presence of a distractor increased RTs from 592 ms without distractor to 613 ms with a face-like happy and 621 ms with a face-like angry distractor, $F(2,30) = 11.27$, $p < 0.001$, $\eta_p^2 = 0.42$. However, the distractor conditions were not significantly different ($p = 0.23$). No significant effects were observed in the accuracy analysis. Overall accuracy was 0.97 (see Table 1).

6.5.2. ERPs to lateralized distractors

Average contra- and ipsilateral ERPs to happy-like and angry-like distractors are shown in Fig. 5. A paired-samples *t*-test showed that the N2pc components in the two distractor conditions did not differ, $p = 0.77$. One-sample *t*-tests against zero showed that the N2pc was neither significant for face-like happy (−0.3 μV), $t(15) = 1.55$, $p = 0.141$, nor for face-like angry distractors (−0.23 μV), $t(15) = 1.54$, $p = 0.144$.

6.6. Discussion

Face-like angry and happy distractors sharing basic features with facial expressions did not capture attention differentially, as indexed by the non-significant difference in the N2pc. Therefore, we conclude that the contribution of low-level factors

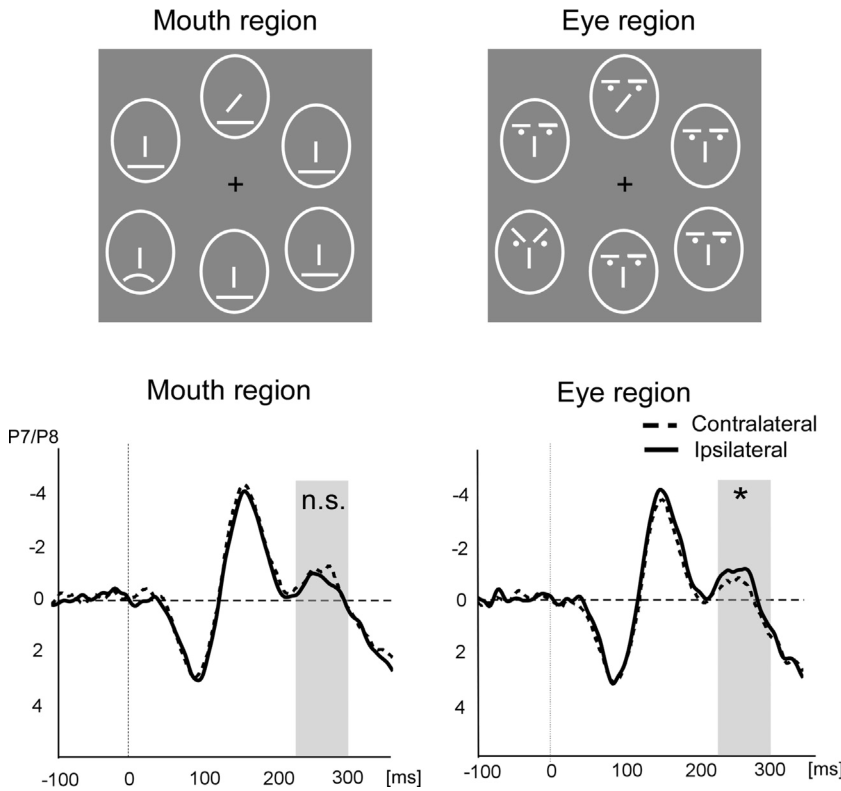

Fig. 4. Top: Sample displays from Experiment 3 in which either the eye region or the mouth region was shown. Bottom: Results from Experiment 3. Note: * = $p < 0.05$ and n.s. = not significant.

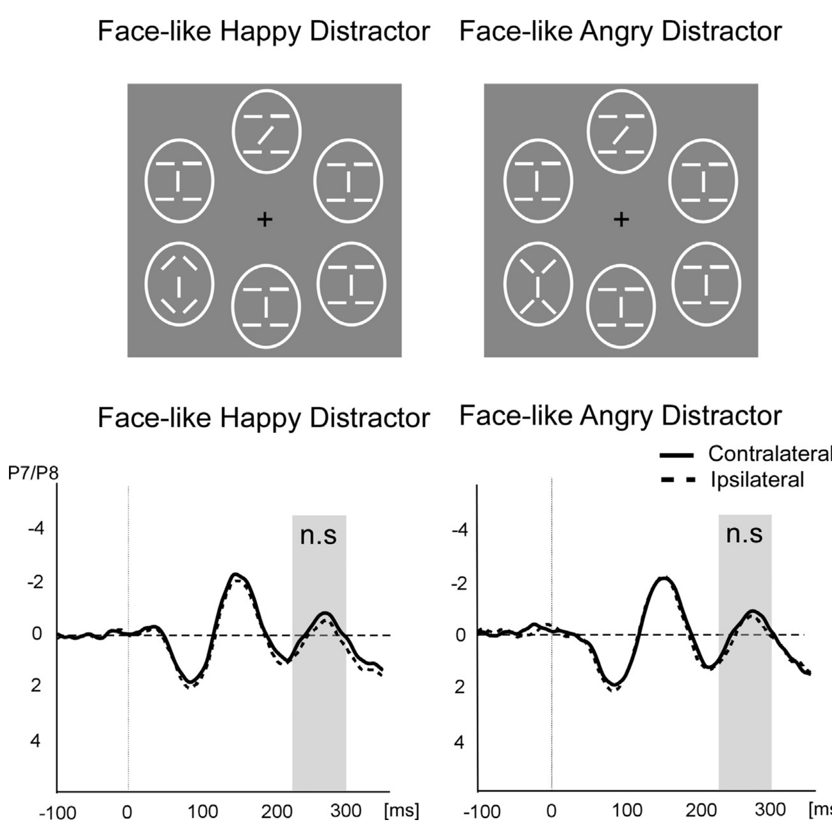

Fig. 5. Top: Sample displays from Experiment 4 that were face-like figures composed of the same lines as in the previous experiments. Bottom: Results from Experiment 3. Note: n.s. = not significant.

to the difference in attentional capture between angry and happy faces that we observed in Experiment 1a is rather minor. Consequently, we claim that the emotional content of angry faces underlies attentional capture and not the associated low-level features.

7. General discussion

We investigated attentional capture by threatening distractors. In a visual search task, we used schematic facial expressions not as a target but as an irrelevant distractor that competed for selection. To our knowledge, previous electrophysiological research has only confirmed facilitated attentional selection of angry target faces. For instance, when facial expressions were used as search targets (Eastwood et al., 2001; Fox et al., 2000; Hansen & Hansen, 1988; Sawada & Sato, 2015), there was no competition between relevant and salient-but-irrelevant elements. Therefore, we pitted search for a relevant facial feature (the nose) against distraction from irrelevant facial features (the eyes and mouth). We demonstrated that attention was captured by angry distractor expressions, but not by happy distractor expressions. This result supports the view that threatening stimuli override current attentional control settings by a specialized "threat-detection system" (Öhman & Mineka, 2001). Attentional capture was indexed by an electrophysiological marker of attentional selection, the N2pc component. As shown in Fig. 6, attentional capture by angry distractors occurred with upright faces, but not with inverted faces (Experiment 2). Additionally, when angry faces were split in eye and mouth regions, attentional capture was only observed for the eye region (Experiment 3). Finally, shapes that shared the basic internal features of emotional facial expressions did not result in differential attentional capture for angry-like faces (Experiment 4).

7.1. Attentional capture by threatening distractors and holistic processing

We have demonstrated that attentional capture by threatening faces occurs when faces are upright. Previously, it has been reported that target discrimination was delayed by facial expressions that were irrelevant for the task without a difference between angry and happy distractors (Hodsoll et al., 2011; Huang et al., 2011). However, previous studies beg the question whether the effect originated at an early perceptual/attentional stage or at a late response-related stage. In fact, some authors concluded that angry faces misguide attention rather than capture attention (Horstmann & Becker, 2008). Whereas the initial shift of involuntary attention is directed to a distractor in attentional capture, voluntary attention is supposed to be biased toward the salient distractor in attentional misguidance. That is, an affective singleton face may receive some attentional priority and weakly attract attention to the target (Todd & Kramer, 1994).

Nevertheless, our results confirm an N2pc to angry facial expressions, showing that threatening stimuli attract attention at an early stage of visual processing. In contrast, no N2pc occurred to happy facial expressions. Therefore, the present results support the attentional capture hypothesis. When processing time was limited by a mask to only 200 ms, stronger distraction by angry than happy expressions was also visible in RTs (see Experiment 1b). With unlimited viewing time, however, RTs did not differ between angry and happy distractor expressions, suggesting that attentional capture by angry expressions was lost in late processing stages. Another interpretation may be that both angry and happy distractors induced similar non-spatial filtering costs that resulted in similar RTs, but that a spatial measure of attentional selectivity, the N2pc, brought differences to the fore (Folk & Remington, 1998; Wykowska & Schubö, 2011). In conclusion, our results are in line with a "threat-detection system", implying that threatening stimuli affect attentional selection (Öhman & Mineka, 2001).

Furthermore, attentional capture by angry distractor expressions only occurred when faces were shown in an upright orientation, which shows that the effect was largely due to the emotional content of angry faces rather than to low-level factors contributing to their saliency (Horstmann, 2007) or to top-down attentional sets for angry faces (Mohanty & Sussman, 2013; Moriya et al., 2014; Todd et al., 2012). Thus, holistic processing (i.e., the perception and characterization of a face as a whole) rather than processing the sum of its individual features is at the core of attentional capture by angry distractor faces in our study. In fact, holistic processing of faces may occur before attentional selection (Towler, Kelly, & Eimer, 2015). Thus, we think that an angry facial expression results in attentional capture because of its emotional content.

7.2. Importance of the eye area in attentional capture by threatening stimuli

Interestingly, the eye region of angry faces is essential to produce attentional capture. This claim is supported by the presence of an N2pc to the eye region and its absence to the mouth region. It has been reported that the eye region (or eyebrows) without the contour of the face does not lead to preferential attentional selection (Weymar et al., 2011). Thus, the anger superiority effect disappeared when faces lack external contours (Schubö et al., 2006). We showed in Experiment 4 that capture by the eye region does not result from low-level features, such as specific orientations or angles, because face-like versions of threatening faces did not show more attentional capture with face-like angry compared to face-like happy stimuli. Experiment 3 suggests that top-down processes enable the perceptual system to perceive the eye area as contained within a whole face (Bentin et al., 2002; Righart et al., 2011). Thus, the angry eyes in a face context trigger attention. Taken together, our data suggest that the eye region underlies attentional capture by angry distractor expressions.

7.3. Face-like stimuli are not sufficient to capture attention

Finally, stimuli created with features sharing their basic organization with facial expressions did not provide evidence for stronger attentional capture by angry compared to happy faces. Some previous results questioned the anger superiority effect by suggesting that the anger superiority effect was mainly the consequence of a low-level difference between stimuli (Becker, Horstmann, & Remington, 2011; Horstmann & Bauland, 2006; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004), such as the closure of the mouth region or the eyebrows with the contour. Indeed, the anger superiority effect has recently been observed using similar face-like stimuli (Coelho et al., 2010; Dickins & Lipp, 2014). Moreover, face-like stimuli are processed in the same way as facial expressions (Armbruster et al., 2014; Larson et al., 2007; Larson et al., 2009; Watson et al., 2011). Overall, these results suggest that low-level perceptual factors account for the anger superiority effect. While our results do not question the validity of previous studies, they nonetheless show that angry expressions may capture attention more strongly even when perceptual factors are controlled for.

Importantly, we demonstrated that face-like angry stimuli do not trigger attentional capture more strongly than face-like happy faces, suggesting a lack of attentional capture by meaningless stimuli despite their similarity with angry faces. Therefore, only facial features seen in the context of faces (whole faces or segmented

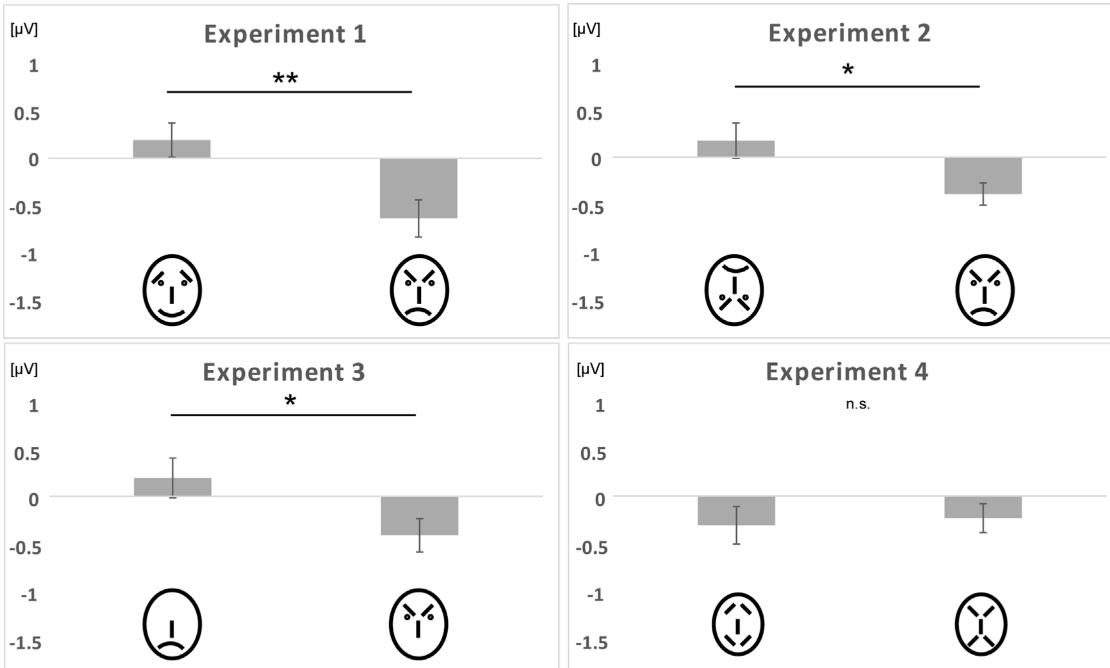

Fig. 6. Summary of distractor N2pc amplitudes (Experiment 1–4). Note: * = $p < 0.05$, ** = $p < 0.01$, and n.s. = not significant.

faces) permit angry faces to gain their emotional content, which contributes crucially to their attentional priority.

7.4. Caveats

The main goal when creating our stimuli was to remove physical differences between schematic faces. To this end, we basically only mirrored the eyebrows and the mouth to create happy and angry faces. Therefore, low-level visual differences cannot account for the larger N2pc to angry distractors. On the flip side, the control of visual stimulus properties may have induced differences in judged valence and intensity (see Appendix A). Thus, the current study is certainly limited in that we cannot entirely rule out confounding effects of intensity. However, an important point is that the valence and intensity of our stimuli were comparable to Coelho et al. (2010) who claimed that low-level features probably underlie the better detection of angry faces. In contrast, we provide evidence that even perceptually balanced stimuli show an "anger superiority" effect. In future studies, valence and intensity should be better controlled, possibly by using natural stimuli. However, this would necessarily come at the cost of re-introducing physical differences between stimuli. The purpose of the present study, however, was to find evidence for stronger attentional capture by angry expressions with perceptually balanced stimuli.

Additionally, we have implied that our task relied on configural face processing. Alternatively, participants may have used a feature-based strategy without processing individual face configurations. Possibly, participants scanned the faces from top to bottom to find the response-relevant feature (the nose), which would explain why the eyes play such a dominant role. In fact, the eyes would be encountered first whereas they are encountered last when the faces are turned upside-down. Consequently, attentional capture would be reduced with upside-down faces, as observed in Experiment 2. However, if the upper parts are crucial and the rest is not, we should have observed an anger superiority effect also with face-like geometrical figures in Experiment 4. The fact that we did not observe a difference between angry-like and happy-like faces speaks against the scanning hypothesis. However, more research is clearly needed to confirm this conclusion.

7.5. Summary

In sum, we propose that the emotional content associated with angry distractor expressions may cause attentional capture. Indeed, angry schematic faces were associated with negative emotional valence, while happy schematic faces were associated with positive valence (see Appendix A). In studies on reward, it has been shown that increasing the intrinsic value of a stimulus leads to an increase of attentional capture (Hickey, Chelazzi, & Theeuwes, 2010; Mine & Saiki, 2015), which modulates the N2pc (Qi, Zeng, Ding, & Li, 2013). Further, angry faces are more relevant for our survival than happy faces because they indicate potentially harmful encounters. Consequently, the threatening and negative emotional content of angry faces might explain attentional deployment to angry expressions even when they are irrelevant. However, the preferential attentional selection of angry distractors might be attenuated after conditioning, which changes the negative valence associated with the facial expression (Yao et al., 2014). In general, we think that the attentional priority of a stimulus in terms of its intrinsic reward- or task-related value (Awh, Belopolsky, & Theeuwes, 2012) is essential to elicit attentional capture and might extend the hypothesis of a "threat-detection system" (Öhman & Mineka, 2001).

Taken together, our experiments demonstrate that irrelevant angry expressions capture spatial attention when competing with the target. In a series of control experiments, we ruled out alternative explanations in terms of low-level factors that have been shown to render angry expressions salient. We conclude that the emotional content of angry expressions may overrule the current task set, resulting in involuntary attentional capture.

Acknowledgements

The authors were supported by the Swiss National Foundation 100014_152684. We thank Laure Freydefont for her constructive comments.

Appendix A

Stimulus Validation

A methodological concern in experiments measuring the N2pc is to equalize the luminance between the visual hemi-fields. Because it is difficult to assure equal luminance with pictures of real faces, we decided to use schematic faces (Öhman et al., 2001; Eastwood et al., 2001; Fox et al., 2000; Lundqvist & Öhman, 2005).

Subsequently, we asked 18 participants to evaluate the schematic facial expressions used in the present and previous studies (Öhman et al., 2001; Coelho et al., 2010; Weymar et al., 2011). Participants were asked to judge the valence (positive – negative) and the intensity (low – high) of these three sets of stimuli on a scale from 1 (positive/low) to 8 (negative/high). The stimuli were presented in printed form and stimulus order was randomized by using three different versions of the questionnaire. We used three different configurations of facial expressions (neutral, angry and happy) and three picture sets. The mean ratings are shown in supplementary Figure A.

Valence

A 3 (picture set: present study, Öhman's, Coelho's) x 3 (facial expression: neutral, angry and happy) repeated-measure ANOVA showed that happy faces were rated as more positive (5.8) than neutral (3.9) and angry (1.3) faces, $F(2,34) = 213.59$, $p < 0.001$. Additionally, our picture set (3.6) and Coelho's (3.37) were judged as less negative than Öhman's (4.1), $F(2,34) = 15.35$, $p < 0.001$. Because the interaction was significant, $F(4,68) = 2.87$, $p = 0.029$, we evaluated effects of picture set separately for each expression (angry, happy, neutral) by one-way ANOVA. Neutral faces were rated more negative in Coehlo's (3.5) than in Öhman's or our picture set (4.1 and 4.2, respectively), $F(2,34) = 6.92$, $p = 0.003$. In contrast, there was no main effect of picture set for angry and happy faces, $ps > 0.98$.

Intensity

The same ANOVA as above revealed that angry faces were rated as more intense (6.7) than happy (5.1) and neutral (3.5) faces, $F(2,34) = 7.98$, $p < 0.005$. Additionally, our picture set (5.2) and Coelho's (5.42) were judged as more intense than Öhman's dataset (4.7), $F(2,34) = 37.99$, $p < 0.001$. Finally, an interaction effect, $F(4,68) = 5.67$, $p < 0.005$, was obtained. Again, we ran separate one-way ANOVAs (picture set: ours, Öhman's, Coelho's) for each expression and found a significant result only for angry expressions. The intensity of angry faces was lower in Öhman's picture set (5.7) than in ours (7.16) and Coelho's (7.33), $F(2,34) = 15.46$, $p < 0.001$.

Discussion

Taken together, our stimuli are similar to stimulus sets used in previous studies concerning their valence and intensity. In contrast, asymmetries between angry and happy faces are apparent, but cannot be removed without introducing physical differences between the stimuli.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biopsycho.2016.08.008.

References

Ansorge, U., Horstmann, G., & Worschech, F. (2010). Attentional capture by masked colour singletons. *Vision Research*, *50*(19), 2015–2027.

Armbruster, D., Suchert, V., Gärtner, A., & Strobel, A. (2014). Threatening shapes: The impact of simple geometric configurations on peripheral physiological markers. *Physiology & Behavior*, *135*, 215–221.

Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences*, *16*(8), 437–443. http://dx.doi.org/10.1016/j.tics.2012.06.010

Baron-Cohen, S. (1997). *Mindblindness: An essay on autism and theory of mind*. MIT press.

Becker, S. I., Horstmann, G., & Remington, R. W. (2011). Perceptual grouping, not emotion, accounts for search asymmetries with schematic faces. *Journal of Experimental Psychology-Human Perception and Performance*, *37*(6), 1739–1757. http://dx.doi.org/10.1037/a0024665

Bentin, S., Sagiv, N., Mecklinger, A., Friederici, A., & von Cramon, Y. D. (2002). Priming visual face-processing mechanisms: Electrophysiological evidence. *Psychological Science*, *13*(2), 190–193.

Bombari, D., Schmid, P. C., Schmid Mast, M., Birri, S., Mast, F. W., & Lobmaier, J. S. (2013). Emotion recognition: The role of featural and configural face information. *Quarterly Journal of Experimental Psychology*, *66*(12), 2426–2442. http://dx.doi.org/10.1080/17470218.2013.789065

Burra, N., & Kerzel, D. (2013). Attentional capture during visual search is attenuated by target predictability: Evidence from the N2pc, Pd, and topographic segmentation. *Psychophysiology*, http://dx.doi.org/10.1111/psyp.12019

Burra, N., & Kerzel, D. (2014). The distractor positivity (Pd) signals lowering of attentional priority: Evidence from event-related potentials and individual differences. *Psychophysiology*.

Calder, A. J., & Jansen, J. (2005). Configural coding of facial expressions: The impact of inversion and photographic negative. *Visual Cognition*, *12*(3), 495–518.

Calder, A. J., Young, A. W., Keane, J., & Dean, M. (2000). Configural information in facial expression perception. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(2), 527.

Calvo, M. G., & Nummenmaa, L. (2008). Detection of emotional faces: Salient physical features guide effective visual search. *Journal of Experimental Psychology-General*, *137*(3), 471–494. http://dx.doi.org/10.1037/a0012771

Coelho, C. M., Cloete, S., & Wallis, G. (2010). The face-in-the-crowd effect: When angry faces are just cross (es). *Journal of Vision*, *10*(1), 7.

Darwin, C. (1872). *The expression of the emotions in man and animals*. Murray.

Dickins, D. S., & Lipp, O. V. (2014). Visual search for schematic emotional faces: angry faces are more than crosses. *Cognition and Emotion*, *28*(1), 98–114.

Eastwood, J. D., Smilek, D., & Merikle, P. M. (2001). Differential attentional guidance by unattended faces expressing positive and negative emotion? *Perception & Psychophysics*, *63*(6), 1004–1013.

Eimer, M., & Kiss, M. (2008). Involuntary attentional capture is determined by task set: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, *20*(8), 1423–1433. http://dx.doi.org/10.1162/jocn.2008.20099

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity? *Electroencephalography and Clinical Neurophysiology*, *99*(3), 225–234.

Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect*. Consulting Psychologists Press.

Elder, J., & Zucker, S. (1993). The effect of contour closure on the rapid discrimination of two-dimensional shapes? *Vision Research*, *33*(7), 981–991.

Elder, J., & Zucker, S. (1994). A measure of closure? *Vision Research*, *34*(24), 3361–3369.

Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance*, *21*(3), 628.

Feldmann-Wüstefeld, T., Schmidt-Daffy, M., & Schubö, A. (2011). Neural evidence for the threat detection advantage: Differential attention allocation to angry and happy faces. *Psychophysiology*, *48*(5), 697–707.

Feldmann-Wüstefeld, T., Uengoer, M., & Schubö, A. (2015). You see what you have learned. Evidence for an interrelation of associative learning and visual selective attention. *Psychophysiology*, *52*(11), 1483–1497.

Folk, C. L., & Remington, R. (1998). Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology-Human Perception and Performance*, *24*(3), 847–858. http://dx.doi.org/10.1037/0096-1523.24.3.847

Fox, E., & Damjanovic, L. (2006). The eyes are sufficient to produce a threat superiority effect. *Emotion*, *6*(3), 534.

Fox, E., Lester, V., Russo, R., Bowles, R. J., Pichler, A., & Dutton, K. (2000). Facial expressions of emotion: Are angry faces detected more efficiently? *Cognition & Emotion*, *14*(1), 61–92. http://dx.doi.org/10.1080/026999300378996

Hahn, S., & Gronlund, S. D. (2007). Top-down guidance in visual search for facial expressions. *Psychonomic Bulletin and Review*, *14*(1), 159–165.

Hansen, C. H., & Hansen, R. D. (1988). Finding the face in the crowd: An anger superiority effect? *Journal of Personality and Social Psychology*, *54*(6), 917–924.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception? *Trends in Cognitive Sciences*, *4*(6), 223–233.

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of Cognitive Neuroscience*, *18*(4), 604–613. http://dx.doi.org/10.1162/jocn.2006.18.4.604

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, *21*(4), 760–775. http://dx.doi.org/10.1162/jocn.2009.21039

Hickey, C., Chelazzi, L., & Theeuwes, J. (2010). Reward changes salience in human vision via the anterior cingulate. *The Journal of Neuroscience*, *30*(33), 11096–11103. http://dx.doi.org/10.1523/jneurosci.1026-10.2010

Hodsoll, S., Viding, E., & Lavie, N. (2011). Attentional capture by irrelevant emotional distractor faces. *Emotion*, *11*(2), 346–353. http://dx.doi.org/10.1037/A0022771

Horstmann, G., & Bauland, A. (2006). Search asymmetries with real faces: Testing the anger-superiority effect. *Emotion*, *6*(2), 193–207. http://dx.doi.org/10.1037/1528-3542.6.2.193

Horstmann, G., & Becker, S. I. (2008). Attentional effects of negative faces: Top-down contingent or involuntary? *Perception & Psychophysics*, *70*(8), 1416–1434. http://dx.doi.org/10.3758/PP.70.8.1416

Horstmann, G., Lipp, O. V., & Becker, S. I. (2012). Of toothy grins and angry snarls—Open mouth displays contribute to efficiency gains in search for emotional faces Horstmann, Lipp, & Becker. *Journal of Vision*, *12*(5) [7–7.

Horstmann, G. (2007). Preattentive face processing: What do visual search experiments with schematic faces tell us? *Visual Cognition*, *15*(7), 799–833. http://dx.doi.org/10.1080/13506280600892798

Huang, S. L., Chang, Y. C., & Chen, Y. J. (2011). Task-irrelevant angry faces capture attention in visual search while modulated by resources. *Emotion*, *11*(3), 544–552. http://dx.doi.org/10.1037/a0022763

Huber-Huber, C., Grubert, A., Ansorge, U., & Eimer, M. (2015). Nasotemporal ERP differences: Evidence for increased inhibition of temporal distractors. *Journal of Neurophysiology*, *113*(7), 2210–2219. http://dx.doi.org/10.1152/jn.00344.2014

Kahneman, D., Treisman, A., & Burkell, J. (1983). The cost of visual filtering? *Journal of Experimental Psychology: Human Perception and Performance*, *9*(4), 510–522.

Kiss, M., Grubert, A., Petersen, A., & Eimer, M. (2012). Attentional capture by salient distractors during visual search is determined by temporal task demands. *Journal of Cognitive Neuroscience*, *24*(3), 749–759. http://dx.doi.org/10.1162/jocn_a_00127

Koster, E. H., Crombez, G., Van Damme, S., Verschuere, B., & De Houwer, J. (2004). Does imminent threat capture and hold attention? *Emotion*, *4*(3), 312–317. http://dx.doi.org/10.1037/1528-3542.4.3.312

Lang, P. J., Davis, M., & Öhman, A. (2000). Fear and anxiety: Animal models and human cognitive psychophysiology. *Journal of Affective Disorders*, *61*(3), 137–159.

Larson, C. L., Aronoff, J., & Stearns, J. J. (2007). The shape of threat: Simple geometric forms evoke rapid and sustained capture of attention. *Emotion*, *7*(3), 526.

Larson, C. L., Aronoff, J., Sarinopoulos, I. C., & Zhu, D. C. (2009). Recognizing threat: A simple geometric shape activates neural circuitry for threat detection? *Journal of Cognitive Neuroscience*, *21*(8), 1523–1535.

LeDoux, J. (1996). Emotional networks and motor control: A fearful view. *Progress in Brain Research*, *107*, 437–446.

Lipp, O. V., Price, S. M., & Tellegen, C. L. (2009). No effect of inversion on attentional and affective processing of facial expressions. *Emotion*, *9*(2), 248–259. http://dx.doi.org/10.1037/a0014715

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology? *Journal of Experimental Psychology: Human Perception and Performance*, *20*(5), 1000–1014.

Luck, S. J. (2005). *An Introduction to the event-related potential technique*. The MIT Press.

Lundqvist, D., & Öhman, A. (2005). Emotion regulates attention: The relation between facial configurations facial emotion, and visual attention. *Visual Cognition*, *12*(1), 51–84.

Mak-Fan, K. M., Thompson, W. F., & Green, R. E. (2011). Visual search for schematic emotional faces risks perceptual confound. *Cognition & Emotion*, *25*(4), 573–584. http://dx.doi.org/10.1080/02699931.2010.500159

McDonald, J. J., Green, J. J., Jannati, A., & Di Lollo, V. (2013). On the electrophysiological evidence for the capture of visual attention. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(3), 849–860. http://dx.doi.org/10.1037/a0030510

Mine, C., & Saiki, J. (2015). Task-irrelevant reward-learning elicits value-driven attentional capture. *Journal of Vision*, *15*(12), 1345. http://dx.doi.org/10.1167/15.12.1345

Moriya, J., Koster, E. H., & De Raedt, R. (2014). The influence of working memory on the anger superiority effect. *Cognition & Emotion*, *28*(8), 1449–1464. http://dx.doi.org/10.1080/02699931.2014.890094

Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, *108*(3), 483–522.

Öhman, A., Lundqvist, D., & Esteves, F. (2001). The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of Personality and Social Psychology*, *80*(3), 381.

Purcell, D. G., & Stewart, A. L. (2010). Still another confounded face in the crowd. *Attention Perception, & Psychophysics*, *72*(8), 2115–2127.

Qi, S., Zeng, Q., Ding, C., & Li, H. (2013). Neural correlates of reward-driven attentional capture in visual search. *Brain Research*, *1532*(0), 32–43. http://dx.doi.org/10.1016/j.brainres.2013.07.044

Righart, R., Burra, N., & Vuilleumier, P. (2011). Face perception in the mind's eye. *Brain Topography*, *24*(1), 9–18. http://dx.doi.org/10.1007/s10548-010-0164-8

Savage, R. A., & Lipp, O. V. (2015). The effect of face inversion on the detection of emotional faces in visual search? *Cognition and Emotion*, *29*(6), 972–991.

Savage, R. A., Lipp, O. V., Craig, B. M., Becker, S. I., & Horstmann, G. (2013). In search of the emotional face: Anger versus happiness superiority in visual search. *Emotion*, *13*(4), 758–768. http://dx.doi.org/10.1037/a0031970

Savage, R. A., Becker, S. I., & Lipp, O. V. (2016). Visual search for emotional expressions: Effect of stimulus set on anger and happiness superiority. *Cognition and Emotion*, *30*(4), 713–730.

Sawada, R., & Sato, W. (2015). Emotional attention capture by facial expressions. *Scientific reports*, *5*, 14042. http://dx.doi.org/10.1038/srep14042

Sawaki, R., & Luck, S. J. (2013). Active suppression after involuntary capture of attention. *Psychonomic Bulletin & Review*, *20*(2), 296–301. http://dx.doi.org/10.3758/s13423-012-0353-4

Schreij, D., Owens, C., & Theeuwes, J. (2008). Abrupt onsets capture attention independent of top-down control settings. *Perception & Psychophysics*, *70*(2), 208–218.

Schubö, A., Gendolla, G. H., Meinecke, C., & Abele, A. E. (2006). Detecting emotional faces and features in a visual search paradigm: Are faces special? *Emotion*, *6*(2), 246–256. http://dx.doi.org/10.1037/1528-3542.6.2.246

Schyns, P. G., & Oliva, A. (1999). Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition*, *69*(3), 243–265.

Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information? *Psychological Science*, *13*(5), 402–409.

Schyns, P. G., Petro, L. S., & Smith, M. L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. *Current Biology*, *17*(18), 1580–1585. http://dx.doi.org/10.1016/j.cub.2007.08.048

Tanaka, J. W., & Farah, J. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology*, *46*(2), 225–245.

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory & Cognition*, *25*(5), 583–592.

Tanaka, J. W., Kaiser, M. D., Butler, S., & Le Grand, R. (2012). Mixed emotions: Holistic and analytic perception of facial expressions. *Cognition and Emotion*, *26*(6), 961–977. http://dx.doi.org/10.1080/02699931.2011.630933

Theeuwes, J. (1992). Perceptual selectivity for color and form? *Perception & Psychophysics*, *51*(6), 599–606.

Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica*, *135*(2), 77–99. http://dx.doi.org/10.1016/j.actpsy.2010.02.006

Tipples, J., Atkinson, A. P., & Young, A. W. (2002). The eyebrow frown: A salient social signal. *Emotion*, *2*(3), 288.

Todd, S., & Kramer, A. F. (1994). Attentional misguidance in visual search? *Perception & Psychophysics*, *56*(2), 198–210.

Todd, R. M., Cunningham, W. A., Anderson, A. K., & Thompson, E. (2012). Affect-biased attention as emotion regulation. *Trends in Cognitive Sciences*, *16*(7), 365–372. http://dx.doi.org/10.1016/j.tics.2012.06.003

Towler, J., Kelly, M., & Eimer, M. (2015). The focus of spatial attention determines the number and precision of face representations in working memory. *Cerebral Cortex*, http://dx.doi.org/10.1093/cercor/bhv083

Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology*, *79*(Pt 4), 471–491.

Vinette, C., Gosselin, F., & Schyns, P. G. (2004). Spatio-temporal dynamics of face recognition in a flash: It's in the eyes. *Cognitive Science*, *28*(2), 289–301. http://dx.doi.org/10.1016/j.cogsci.2004.01.002

Vogt, J., De Houwer, J., Crombez, G., & Van Damme, S. (2013). Competing for attentional priority: Temporary goals versus threats. *Emotion*, *13*(3), 587–598. http://dx.doi.org/10.1037/a0027204

Watson, D. G., Blagrove, E., & Selwood, S. (2011). Emotional triangles: A test of emotion-based attentional capture by simple geometric shapes. *Cognition & Emotion*, *25*(7), 1149–1164.

Weymar, M., Löw, A., Öhman, A., & Hamm, A. O. (2011). The face is more than its parts – Brain dynamics of enhanced spatial attention to schematic threat. *Neuroimage*, *58*(3), 946–954. http://dx.doi.org/10.1016/j.neuroimage.2011.06.061

Wolfe, J. M., & Horowitz, T. S. (2004). What attributes guide the deployment of visual attention and how do they do it? *Nature Reviews Neuroscience*, *5*(6), 495–501.

Wykowska, A., & Schubö, A. (2011). Irrelevant singletons in visual search do not capture attention but can produce nonspatial filtering costs. *Journal of Cognitive Neuroscience*, *23*(3), 645–660. http://dx.doi.org/10.1162/jocn.2009.21390

Yao, S., Ding, C., Qi, S., & Yang, D. (2013). The anger superiority effect in the discrimination task is independent of temporal task demands. *Neuroscience Letters*, *548*, 275–279. http://dx.doi.org/10.1016/j.neulet.2013.06.006

Yao, S., Ding, C., Qi, S., & Yang, D. (2014). Value associations of emotional faces can modify the anger superiority effect: Behavioral and electrophysiological evidence. *Social Cognitive and Affective Neuroscience*, *9*(6), 849–856.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*(1), 141.