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Giovanni Galfano^a; Michela Sarlo^a; Federica Sassi^b; Marianna Munafò^a; Luis J. Fuentes^b; Carlo Umiltà^a ^a Università di Padova, Padova, Italy ^b Universidad de Murcia, Murcia, Spain

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Reorienting of spatial attention in gaze cuing is reflected in N2pc

Giovanni Galfano, and Michela Sarlo

Università di Padova, Padova, Italy

Federica Sassi

Universidad de Murcia, Murcia, Spain

Marianna Munafò

Università di Padova, Padova, Italy

Luis J. Fuentes

Universidad de Murcia, Murcia, Spain

Carlo Umiltà

Università di Padova, Padova, Italy

Research has shown that gaze cuing of attention is reflected in the modulation of P1 and N1 components of ERPs time-locked to target onset. Studies focusing on cue-locked analyses have produced mixed results. The present study examined ERP reflections of gaze cuing in further detail by recording electric brain activity from the scalp of participants engaged in a spatial cuing paradigm with noninformative gaze cues embedded in fearful, disgusted, or neutral faces. Unlike previous work, we focused on N2pc, a recent ERP index of attention shifting over space. Behavioral data showed that gaze-driven orienting was not influenced by facial expression. Importantly, electrophysiological data showed a significant amplitude modulation of the N2pc time-locked to target onset as a function of cue-target spatial congruence. This pattern, however, was independent of facial expression. The results are interpreted as evidence that N2pc can be used as a marker of reorienting of attention in spatially incongruent trials due to gaze cuing. The overall findings support the idea that the effects of facial expression on gaze cuing are weak and likely context-dependent.

Keywords: Gaze cuing; Emotion; Attention; N2pc.

INTRODUCTION

Eye gaze is an important stimulus in everyday life, because it conveys information that may help the observer to understand the mental states and behavioral intentions of others, and potentially can signal the presence of threats or other relevant stimuli outside our current focus of attention (for reviews see Frischen, Bayliss, & Tipper, 2007; Itier & Batty, 2009; Nummenmaa & Calder, 2009).

In the present study, we focused on gaze cuing, the phenomenon whereby individuals presented with a face

Correspondence should be addressed to: Giovanni Galfano, Dipartimento di Psicologia dello Sviluppo e della Socializzazione, Università di Padova, via Venezia, 8, I-35131, Padova, Italy. E-mail: giovanni.galfano@unipd.it

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showing a task-irrelevant averted eye gaze prior to the onset of a lateralized target tend to produce covert shifts of attention in the corresponding direction (e.g., Driver et al., 1999; Friesen & Kingstone, 1998; Hietanen, 1999). Despite the strong interest in gaze cuing with classic behavioral measures, few studies so far have attempted to clarify spatial attention dynamics driven by eye gaze using event-related brain potentials (ERPs). Most studies (e.g., Schuller & Rossion, 2001, 2004; Tipper, Handy, Giesbrecht, & Kingstone, 2008) reported enhanced P1 and N1 responses for cued trials (i.e., trials in which the target appeared in the gazed-at location) compared to uncued trials (i.e., trials in which the target appeared in the nongazed-at location), consistent with the view that spatial cues produce an early enhancement of visual input achieved through the allocation of attentional resources (Luck, Woodman, & Vogel, 2000). Hietanen, Leppänen, Nummenmaa, and Astikainen (2008) measured ERPs time-locked to cue onset and showed that, unlike attention shifting induced by arrows, gaze-driven orienting was not associated to a modulation of the so-called early directing attention negativity (EDAN; see also Holmes, Mogg, Monje Garcia, & Bradley, 2010). This finding is consistent with recent neuroimaging reports (e.g., Engell et al., in press; Hooker et al., 2003) showing that gaze and symbolic cues (i.e., arrows) differentially recruit the dorsal and ventral attention networks that have been associated with goal-directed and stimulus-driven orienting, respectively (e.g., Thiel, Zilles, & Fink, 2004). More recently, however, Brignani, Guzzon, Marzi, and Miniussi (2009) have reported an anticipated amplitude modulation, with gaze cues associated with a reversed EDAN-like effect. Because of these mixed results, and because the view that EDAN genuinely reflects (exogenous) shifts of attention is far from being universally accepted (e.g., Van Velzen & Eimer, 2003; Woodman, Arita, & Luck, 2009), in the present study we focused on a more recent ERP index of spatial attention shifts, that is N2pc (N2 posterior contralateral), a component that is thought to reflect allocation of attention in the spatial domain (Eimer, 1996; Luck & Hillyard, 1994a, 1994b).

N2pc usually arises at posttarget latencies of 180–300 ms, and consists of a more pronounced negative activity in the posterior sites contralateral to the side of the target stimulus (e.g., Luck, 2005; Mazza, Turatto, Umiltà, & Eimer, 2007). Unlike classic ERP components that have been linked to attentional processes (e.g., P1), N2pc is isolated by subtracting brain activity at electrode sites ipsilateral to the target from the corresponding activity at electrode sites contralateral to the target. The precise nature of the specific processes underlying the N2pc is still under debate,

with some studies arguing that this component reflects distractor suppression mechanisms (e.g., Luck & Hillyard, 1994b) and others holding that it reflects target enhancement processes (e.g., Eimer, 1996; Mazza, Turatto, & Caramazza, 2009). Although the functional significance of the N2pc has yet to be fully understood, robust links have been established between the presence of this component and attentional selection in space. In addition, despite the fact that N2pc has mostly been investigated with visual search tasks (e.g., Eimer & Kiss, 2007; Luck & Hillyard, 1994b; Mazza et al., 2007), several studies have been reported using different experimental paradigms that make N2pc a wellvalidated index of spatial selection (e.g., Buodo, Sarlo, & Munafò, 2010; Dell'Acqua, Sessa, Jolicoeur, & Robitaille, 2006; Fox, Derakshan, & Shoker, 2008; Holmes, Bradley, Kragh Nielsen, & Mogg, 2009). In particular, Woodman et al. (2009) have recently demonstrated that the N2pc can be observed in spatial cuing paradigms. They used centrally displayed spatial cues (words informing the participants about the correct location of the upcoming target stimulus with 100% validity) and reported a significant posterior contralateral negativity in the time range of the N2pc timelocked to target onset. Critically, Woodman et al. did not observe any EDAN-like component shortly after cue onset, a finding that seems inconsistent with the view that EDAN reflects attention shifts to the cued location. No evidence has been reported so far showing that covert orienting driven by eye gaze is reflected in an N2pc modulation. The first aim of the present study was to fill this gap. Because the N2pc was measured time-locked to target onset, we reasoned that if the N2pc mirrors (at least partially) the shift of attention to the target location (see Woodman et al., 2009), then its amplitude should be attenuated in spatially congruent trials relative to spatially incongruent trials, since attention should be at the correct location at target onset in spatially congruent trials, and therefore should not need to shift again in these trials, contrary to spatially incongruent trials. Hence, the general prediction in the present study was to observe a larger N2pc for uncued (i.e., nongazed-at) than for cued (i.e., gazedat) targets, reflecting reorienting of attention towards the real target location as a result of the previous shift of attention to the location signaled by eye gaze (also see Brisson & Jolicoeur, 2008, for a similar logic with a different spatial cuing task). Because in spatially incongruent trials attention would be misdirected by gaze over the location opposite to the target, the N2pc would index the attention shift needed to reorient attention to the target location.

The second aim of the present study was to address possible gaze-cuing modulations of N2pc as a function

of emotional expression of the face displaying the averted gaze. Previous behavioral research on this topic has produced mixed results, with some studies reporting no interactions (e.g., Bayliss, Frischen, Fenske, & Tipper, 2007; Hietanen & Leppänen, 2003) and others reporting larger gaze-cuing effects for fearful faces, at least in participants with high levels of anxiety and fearfulness (e.g., Fox, Mathews, Calder, & Yiend, 2007; Putman, Hermans, & van Honk, 2006; Tipples, 2006). Recent ERP investigations (Fichtenholtz, Hopfinger, Graham, Detwiler, & LaBar, 2007, 2009) focusing on classic ERP components related to attention shifting time-locked to target onset have again produced mixed results. In behavioral measures, gazecuing effects were consistently similar independent of facial expression. On the ERP side, no differences emerged in early components, whereas a significant interaction between facial expression and cuing was observed for the P3 complex, due to a larger P3 response for nongazed-at (i.e., uncued) than for gazed-at (i.e., cued) targets for fearful but not for happy faces. Fichtenholtz et al. (2007) have argued that because the P3 is thought to index contextual updating processes (Mangun & Hillyard, 1991), the pattern they observed may reflect the contextual advantage of the fearful expression for shifting attention to the gazed-at location. In another study, however, Fichtenholtz et al. (2009) used the same paradigm with neutral and fearful faces, and no evidence of facial expression × cuing interaction emerged as regards the P3 complex. That suggests that emotional expression and gaze direction exerted independent influence over attentional orienting.

In the present study, real faces were used, appearing with fearful, disgusted, and neutral expressions. As regards the possible effects of emotion on gazedriven orienting, disgust and fear were contrasted under the hypothesis that these emotional expressions, which are known to recruit distinct neural circuits (e.g., Phillips et al., 1998; Santos, Iglesias, Olivares, & Young, 2008), may induce opposite effects on attention shifting, based on the consideration that they may be placed towards opposite poles along an attentionrejection dimension (e.g., Schlosberg, 1954), and that they are known to modulate distinct cognitive processes (e.g., Olatunji, Cisler, Meunier, Connolly, & Lohr, 2008). On one hand, a fearful expression associated to an averted gaze may increase likelihood of attention shifting in the corresponding direction as gaze may potentially signal the location of a threat. This possibility is supported by studies demonstrating larger gaze-cuing effects for fearful faces with respect to neutral faces (e.g., Fox et al., 2007; but see, e.g., Holmes et al., 2010). On the other hand, a disgusted expression associated to an averted gaze may decrease likelihood of attention shifting in the corresponding direction as gaze, in this case, may signal the location of a harmless, though aversive, stimulus. This possibility is admittedly more speculative because the effects of a disgusted face on gaze cuing have not been investigated in much detail. Bayliss et al. (2007) reported no gaze-cuing effects for disgusted faces, whereas Pecchinenda, Pes, Ferlazzo, and Zoccolotti (2008) reported a significant gaze-driven orienting effect of similar magnitude for both fearful and disgusted faces. In the present study, we also used a neutral expression condition, which served as a baseline.

Our experimental paradigm was a standard version of the gaze-cuing procedure (see, e.g, Driver et al., 1999), with a fixed 200 ms cue-target stimulus onset asynchrony (SOA). This was done to tap onto exogenous orienting, which is known to rely on a fast-operating mechanism. In addition, a pilot study, in which longer SOA were also present, showed that behavioral effects were strongest with a brief SOA. Similarly to Fichtenholtz et al. (2007, 2009) we used real faces to increase ecological validity. Although our main focus was on the N2pc component, control analyses were also performed that included amplitude of the P1 and N1 components time-locked to target onset, and analyses of the ERP activity time-locked to cue onset.

METHODS

Participants

Twenty-three healthy undergraduate students at the University of Padova (all right-handed by self-report, 15 females) participated in the experiment for either course credits or money compensation (€13 for the whole experimental session, lasting approximately 2 h). All participants gave written informed consent approved by the ethical committee at the University of Padova prior to taking part in the experiment. All reported normal or corrected-to-normal vision. Data from two participants were excluded because of too many EEG recording artifacts, leaving 21 participants for the

¹Because there is evidence that the magnified gaze-driven orienting effect in fearful faces may be particularly visible in high-anxious individuals (e.g., Mathews, Fox, Yiend, & Calder, 2003), our participants were also administered the State–Trait Anxiety Inventory (Spielberger, 1983). Because neither behavioral nor ERP data showed any correlation with the individual scores of the questionnaire, these analyses will not be reported or discussed further (also see Holmes et al., 2010).

analyses (age range 19–47 years; M = 25.13, SD = 6.25). The experiment was conducted in accordance with the Declaration of Helsinki.

Apparatus, stimuli, and procedure

Eight face stimuli were selected from the NimStim Set of Facial Expressions (available at www.macbrain.org/faces, see Tottenham et al., 2009). These consisted of fearful, disgusted, and neutral prototypical expressions posed by eight models (four female and four male, numbered: 01f, 03f, 06f, 10f, 21m, 28m, 33m, 34m). Eight stimuli were used in order to decrease the likelihood of habituation effects that might have played a role in shaping the results reported by Fichtenholtz et al. (2007, 2009). To increase ecological validity, face stimuli appeared in full color.

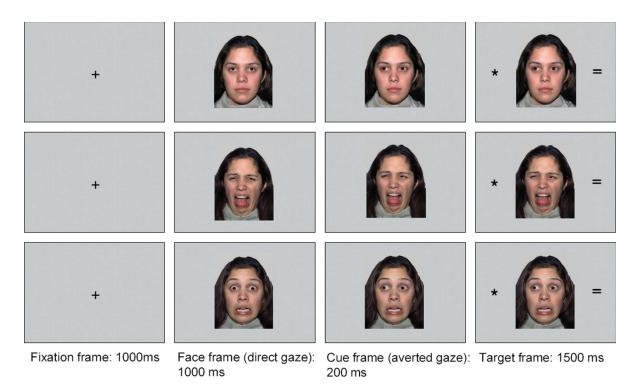
The experiment and the recordings took place in a sound-attenuated, electrically shielded, dimly lit room. A Pentium III PC and E-Prime software (Version 1.2, Psychology Software Tools, Pittsburgh, PA) were used for administering the task, controlling the timing of events, and recording reaction times (RTs) and accuracy of response. Participants sat 70 cm from a 17 inch monitor (1024 × 768, 85 Hz). Target stimuli appeared in black against a gray background. During the fixation frame, a fixation cross $(0.82^{\circ} \text{ width} \times 0.82^{\circ} \text{ height})$ was presented in the center of the screen. The face frame consisted of the onset of a face stimulus (13.65° width \times 16.70° height) centered on the screen and displaying straight gaze along with one of three equiprobable facial expressions (fear, disgust, or neutral). During the cue frame, the same photograph shown in the face frame was visible, except that gaze was averted. Adobe Photoshop was used to create images with irises of both eyes averted (on average 0.25° from the centrally positioned irises in the faces with straight gaze). In the target frame, two symmetrically located symbols (0.82° width \times 0.82° height) appeared simultaneously and aligned with the horizontal meridian. Their inner edges were 10.92° left and right from the center of the screen. The symbols ("=" and "*") were set in 30-point Courier New bold font. One such symbol always served as target stimulus, and the other as distractor stimulus. Which symbol served as target or distractor was counterbalanced across participants. Target appeared left and right of fixation equally often. It is important to note that although spatial cuing experiments generally involve presentation of a single stimulus (i.e., the target), we included also a distractor stimulus because there is evidence that no N2pc occurs when the target is presented in isolation (e.g., Luck & Hillyard, 1994b).

Each trial started with the fixation frame (see Figure 1). After 1000 ms, the fixation cross was replaced by one of the eight faces with straight eyes, and a neutral, disgusted, or fearful expression. After 1000 ms, the cue frame followed, in which the eyes of the face became averted. The target and distractor were shown after a 200 ms SOA, and remained visible, along with the face showing the averted gaze, until a response was made or 1500 ms had elapsed. The participants performed a speeded manual localization task by pressing one of two horizontally aligned keys of the keyboard ("D" and "L") depending on target location. They rested one index finger on each assigned key. The target had the same probability to appear left or right with respect to the face stimulus, irrespective of gaze direction.

Participants performed 5 blocks of 192 trials each. On each block, there was an equal number of trials (96) in which the target appeared at the gazed-at (i.e., spatially congruent) and nongazed-at (i.e., spatially incongruent) locations. For both spatially congruent and spatially incongruent trials, there was an equal number of trials (32) with a fearful, disgusted, and neutral facial expression. In a block, there were 4 trials for each face stimulus for each level of facial expression and spatial congruency between cue direction and target location. Prior to the experimental session, participants performed 20 randomly chosen practice trials. Participants were explicitly informed that neither gaze direction nor facial expression provided information about target location and that they were irrelevant for the task at hand. They were asked to maintain fixation of the center of the screen throughout a trial and to respond as quickly as possible while maintaining accuracy. They were also instructed to avoid making any movements except for responding. They were allowed to take a short break at the end of each block of trials.

ERP recordings and data analyses

The electroencephalogram (EEG) was recorded from 19 tin electrodes mounted in an elastic cap according to the International 10–20 System (Jasper, 1958) at sites FP1, FP2, F3, Fz, F4, F7, F8, C3, Cz, C4, T3, T4, T5, T6, P3, Pz, P4, O1, O2, and right mastoid. The signals were recorded using a left mastoid reference, and then re-referenced offline to the average of the left and right mastoids. For the purpose of artifact scoring, vertical and horizontal electrooculograms (EOGs) were recorded. Electrode pairs (bipolar) were placed at the supraorbit and suborbit of the right eye and at the external canthi of the eyes. All electrode impedances were kept below 10 k Ω . The EEG and



Time

Figure 1. Sequence of events in the experiment. Participants had to perform a spatial localization task and press a key corresponding to target location while ignoring the distractor stimulus. Example trials with a neutral, disgusted, and fearful face are shown in the upper, middle, and lower part of the figure respectively. For participants instructed that the "=" symbol was the target stimulus, the figure illustrates spatially incongruent trials, because the target appears at the nongazed-at (i.e., uncued) locations. For participants instructed that the "*" symbol was the target, the figure illustrates spatially congruent trials. Participants were informed that gaze direction was uninformative as to target location. Stimuli are not drawn to scale.

EOG signals were amplified with Neuroscan Synamps (El Paso, TX), bandpass filtered (0.1–40 Hz), digitized at 250 Hz (16 bit AD converter, accuracy 0.08 μ V/bit) and stored on to a Pentium IV computer.

Continuous EEG data were corrected for eye-blinks using a regression-based correction algorithm (Scan 4.1 software; also see Semlitsch, Anderer, Schuster, & Presslich, 1986). For target-locked analyses, the EEG was then segmented offline into 700 ms epochs from 100 ms before to 600 ms after target onset. For cuelocked analyses, the EEG then segmented offline into 350 ms epochs from 100 ms before to 250 ms after cue onset. The EEG epochs were baseline-corrected against the mean voltage during the 100 ms pretarget (for target-locked analyses) and precue (for cue-locked analyses) periods. All EEG epochs were visually scored for eye movement and other artifacts, and each portion of data containing artifacts greater than ±70 µV in any channel was rejected for all the recorded channels prior to further analysis. For the 21 participants included in the analyses, a maximum of 5.89% of trials per condition were excluded due to artifacts. The percentage of trials that had to be excluded did not change significantly across conditions (p > .05). Artifact-free trials with correct behavioral responses were separately averaged for each participant in each experimental condition.

The N2pc was quantified on the basis of ERP mean amplitudes measured in the 200-300 ms posttarget time window at electrode sites T5/T6, where N2pc had the maximum amplitude (also see Jolicoeur, Sessa, Dell'Acqua, & Robitaille, 2006). N2pc contralaterality scores were obtained by subtracting the mean amplitude recorded from the ipsilateral electrode (with respect to the visual field of the target stimulus) from that of the contralateral electrode. On the basis of visual inspection of grand average ERP waveforms, additional ERP components time-locked to target onset were analyzed at posterior electrode sites (P3/4, T5/6, O1/2): (1) a positive deflection (P1), specified as the most positive peak between 100 and 150 ms from target onset; and (2) a negative deflection (N1), specified as the most negative peak between 150 and 220 ms from target onset.

In addition, a component was also identified after cue onset at posterior electrode sites: a negative deflection (N170), peaking at about 170 ms (Bentin, Allison, Puce, Perez, & McCarthy, 1996). This was defined as the most negative peak between 140 and 190 ms. This analysis was performed as a control for establishing whether gaze direction and emotional expression showed possible interactive effects before target onset. We focused on the N170, because this component is known to be sensitive to apparent motion of the eyes (Puce, Smith, & Allison, 2000).

For all analyses, the Huynh-Feldt correction was applied when sphericity assumptions were violated. In these cases, the uncorrected degrees of freedom and the corrected probability levels are reported. Follow-up comparisons of ERP effects were carried out by means of post-hoc comparisons conducted with the Newman-Keuls test (using a p < .05 criterion for significance).

As a final analysis, we carried out a correlation analysis between behavioral and N2pc data in order to better clarify the functional meaning of the N2pc in response to targets. We subtracted both RTs and percentage of correct responses for spatially congruent trials from RTs and percentage of correct responses for spatially incongruent trials. More positive values in these indices indicate a stronger gaze-cuing effect in RTs and accuracy respectively. On the electrophysiological side, waveform differences were computed for N2pc, by subtracting mean N2pc amplitudes of spatially congruent trials from mean amplitudes of spatially incongruent trials. Then correlation analyses were performed between behavioral and ERP indexes. Significant positive correlations between the behavioral indexes of gaze cuing and the corresponding N2pc index would indicate that participants with higher behavioral gazedriven orienting show larger amplitudes in the spatially incongruent condition compared with the spatially congruent condition.

RESULTS

Behavioral data

Accuracy

A two-way repeated-measures analysis of variance (ANOVA), with cue-target congruency (congruent vs. incongruent) and emotional expression (fearful, disgusted, and neutral) as factors was conducted on mean percentage of correct responses. It revealed a significant main effect of cue-target congruency,

TABLE 1

Mean reaction times (RTs, ms) and percentage of correct responses to left and right targets as a function of face emotional expression and gaze direction

		Target location			
Facial expression - Gaze direction		Left		Right	
		RT	% correct	RT	% correct
Disgust	Left	417 (12)	97.62 (0.64)	418 (11)	96.25 (0.9)
	Right	424 (11)	96.73 (0.92)	407 (12)	98.21 (0.46)
Neutral	Left	414 (12)	97.5 (0.59)	417 (12)	96.61 (0.87)
	Right	423 (12)	96.55 (0.84)	407 (12)	98.81 (0.28)
Fear	Left	412 (12)	97.98 (0.46)	414 (12)	97.26 (0.65)
	Right	422 (11)	96.61 (0.82)	406 (13)	97.5 (0.42)

Standard errors are given in parentheses.

F(1, 20) = 6.717, MSE = 20.682, p < .05, as participants were significantly more accurate when targets were preceded by a congruent gaze (M = 98.02, SE = 0.28) than by an incongruent gaze (M = 96.91, SE = 0.63). Neither the main effect of emotional expression nor the two-way interaction was significant (lowest p > .3). Accuracy data are presented in Table 1, as a function of gaze direction, target location, and emotional expression.

RT

Mean RTs for correct responses were submitted to a two-way repeated-measures ANOVA, with the same factors as the ANOVA on percentage of correct responses. It only revealed a significant main effect of cue-target congruency, F(1, 20) = 19.827, MSE = 127, p < .005, reflecting a gaze-cuing effect, as participants were significantly faster when targets were preceded by a congruent gaze (M = 411 ms, SE = 11) than by an incongruent gaze (M = 420 ms, SE = 10). Neither the main effect of emotional expression nor the two-way interaction was significant (p > .13). RT data are shown in Table 1, as a function of gaze direction, target location, and emotional expression.

ERP data: Target-locked analyses

N2pc

Figure 2 shows grand-averaged ERPs time-locked to target stimuli at occipito-temporal and occipital sites for spatially congruent and incongruent target locations as a function of fearful, neutral, and disgusted facial expressions.

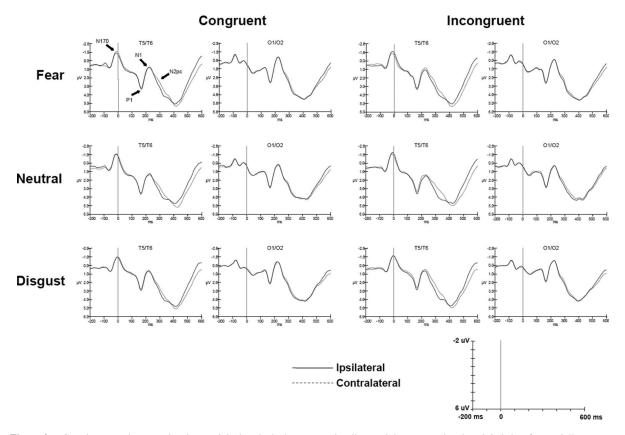


Figure 2. Grand-averaged event-related potentials time-locked to target stimuli at occipito-temporal and occipital sites for spatially congruent and incongruent target locations as a function of fearful, neutral and disgusted facial expressions. Ipsilateral and contralateral refer to the side of target presentation. The vertical gray rule represents target onset. –200 ms refers to cue onset

Figure 3 illustrates difference waveforms obtained by subtracting the ERP mean amplitude measured at the electrode ipsilateral to the target stimulus from that of the contralateral electrode for spatially congruent (solid lines) and incongruent (dashed lines) target locations as a function of disgusted, neutral, and fearful facial expressions.

An omnibus ANOVA was conducted on mean amplitude contralaterality scores in the 200-300 ms posttarget time window with target location (left vs. right), cue-target congruency (congruent vs. incongruent), and emotional expression (fearful, disgusted, and neutral) as factors. It revealed a significant main effect of target location, F(1, 20) = 8.259, MSE =38.695 p < .005, due to a larger N2pc for targets appearing in the right than in the left visual field. Crucially, a significant main effect of cue-target congruency also emerged, F(1, 20) = 14.498, MSE = 0.669, p < .005, as N2pc was larger for targets appearing at spatially incongruent locations than at gazed-at locations. Finally, there was a significant target location \times emotional expression interaction, F(2, 40) = 4.351, MSE = 0.920, p < .05. Post-hoc comparisons showed that this reflected that N2pc was lower in response to

fearful faces than to both disgusted and neutral faces, but only for targets presented in the right visual field. This pattern of effects was confirmed by additional ANOVAs conducted within two smaller successive time windows (early N2pc: 200-250 ms poststimulus; late N2pc: 250-300 ms poststimulus) with the same factors as in the omnibus ANOVA. As regards the early N2pc, target location was significant, F(1, 20) = 11.030, MSE = 39.781, p < .005, due to a larger N2pc for targets appearing in the right than in the left visual field. Cue-target congruency was also significant, F(1, 20) = 11.382, MSE = 0.934, p < .005, confirming that N2pc was more pronounced for targets appearing at spatially incongruent locations than at gazed-at locations. The target location × emotional expression interaction was also significant, F(2, 40)= 3.492, MSE = 1.081, p = .05, and showed the same pattern as that emerged in the omnibus ANOVA. The ANOVA on the late N2pc revealed a significant main effect of cue-target congruency, F(1, 20) = 9.666, MSE = 0.854, p < .01, and a significant target location \times emotional expression interaction, F(2, 40) = 3.910, MSE = 1.096, p < .05, in line with the previous analyses.

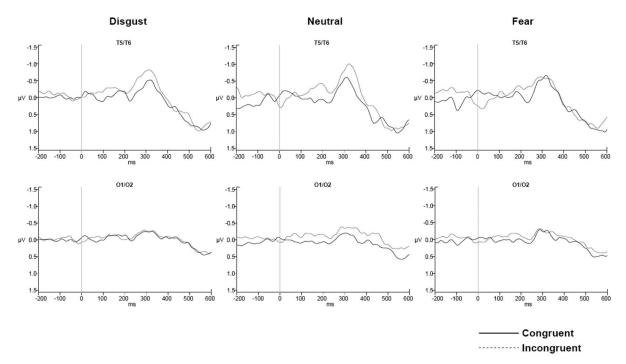


Figure 3. Difference waveforms at occipital and temporal sites obtained by subtracting the ERP mean amplitude measured at the electrode ipsilateral to the target stimulus from that of the contralateral electrode, for spatially congruent and incongruent target locations as a function of disgusted, neutral, and fearful facial expressions. The vertical gray rule represents target onset. –200 ms refers to cue onset.

P1

An omnibus five-way repeated measures ANOVA was conducted on mean amplitude values with target location (left vs. right), cue—target congruency (congruent vs. incongruent), emotional expression (fearful, disgusted, and neutral), electrode cluster (P3–P4, T5–T6, and O1–O2), and hemisphere (left vs. right) as factors. Only the effects that are relevant for the purpose of the study are reported.

The ANOVA revealed a significant main effect of emotional expression, F(2, 40) = 13.745, MSE = 211.555, p < .001, reflecting a larger P1 in response to both fearful and neutral faces with respect to disgusted faces. Critically, neither the main effect of cue–target congruency nor the cue–target congruency × emotional expression interaction were significant (lowest p = .85).

N1

An omnibus five-way repeated measures ANOVA was conducted on mean amplitude values with same factors as the ANOVA for the P1. It revealed a significant main effect of emotional expression, F(2, 40) = 8.670, MSE = 273.459, p < .005, with a greater N1 amplitude in response to either a fearful or disgusted faces than a neutral face. Critically, neither the main

effect of cue-target congruency nor the cue-target congruency \times emotional expression interaction was significant (lowest p = .63).

ERP data: Cue-locked analyses

N170

The N170 was addressed on temporal electrodes only, as it is maximal at these sites (Bentin et al., 1996). The ANOVA revealed a significant main effect of gaze direction, F(1, 20) = 7.536, MSE = 5.182, p < .05, with a greater N170 amplitude in response to a gaze pointing leftwards than rightwards. A significant main effect of emotional expression was also observed, F(2, 40) = 8.080, MSE = 17.549, p < .005. Post-hoc analyses revealed that N170 was smaller after a disgusted face than after either a neutral or a fearful face. A significant gaze direction × hemisphere interaction was also observed, F(1, 20) = 3.686, MSE = 23.808, p < .001. Post-hoc comparisons revealed that N170 was greater over the right than over the left hemisphere independent of gaze direction. However, this asymmetrical amplitude pattern was significantly more pronounced for a leftwards-gazing face than for a rightwards-gazing face.

Correlations between behavioral measures and N2pc amplitude

The magnitude of gaze cuing in RTs was not correlated with the amplitude differences in N2pc between spatially congruent and incongruent trials (r = -.28, p = .21). However, a significant positive correlation was observed between the magnitude of gaze cuing in percentage of correct responses and the amplitude difference between spatially congruent and incongruent trials (r = .48, p < .05), so that a larger gaze-cuing effect was associated to a higher increase in amplitude for the spatially incongruent trials with respect to spatially congruent trials.

DISCUSSION

The present study had two main purposes. First, we aimed to test the possibility that N2pc can be used to map allocation of spatial attention in a gaze-cuing paradigm. Second, we aimed to clarify the influence of eye gaze and emotion expression on spatial attention dynamics by means of ERPs. To this end, we compared gaze-driven orienting in fearful, disgusted, and neutral faces.

On the behavioral side, the results showed a robust gaze-driven orienting effect, with participants performing better (in terms of both accuracy and latency) when the target appeared at the gazed-at location than at the nongazed-at location. In light of the brief SOA (200 ms), this shows that the stimuli employed in the present study were effective in eliciting attention shifts towards the location congruent with gaze direction, despite participants being informed that gaze direction was uninformative as target location. In line with previous behavioral reports, the magnitude of gaze-driven orienting was unaffected by whether the face was fearful (e.g., Fichtenholtz et al., 2009; Hietanen & Leppänen, 2003) or disgusted (e.g., Pecchinenda et al., 2008) compared to neutral. In contrast to Fichtenholtz et al. (2009), no main effect of emotional expression was observed. This is likely due to the fact that Fichtenholtz et al. used a dynamic expression change procedure from neutral to fearful, and the target appeared shortly after the unmasking of emotional expression, whereas in the present study, faces appeared with emotional expressions long before target onset. We suspect that by the time the target appeared, the possible alertness effects of emotional expression on target processing had vanished.

On the electrophysiological side, gaze cuing was accompanied by a significant modulation of N2pc amplitude. Specifically, consistent with our hypotheses,

N2pc amplitude was more pronounced in spatially incongruent than in spatially congruent trials. The behavioral pattern with better performance in spatially congruent over spatially incongruent trials is explained by the fact that, when the target is shown, in spatially congruent trials attention is located on target location already, driven by gaze direction (see Figure 4 for an illustration of the possible attention dynamics). By contrast, in spatially incongruent trials, attention is mislocated by gaze over the distractor location, and an additional shift of attention is necessary to reorient over the target, located over the opposite visual field. Because N2pc is a reliable index to track rapid shifts of spatial attention (e.g., Eimer & Kiss, 2007; Holmes et al., 2009; Woodman & Luck, 1999; Woodman et al., 2009), the amplitude modulation reported in the present study is interpreted as reflecting this additional shift of attention towards the target due to attention having been misdirected by gaze in spatially incongruent trials. In addition to N2pc, we also analyzed classic P1 and N1 components, whose amplitude has been shown to be modulated as a function of cue-target congruency in gaze-cuing paradigms (Schuller & Rossion, 2001, 2004). However, cue-target congruency did not impact either P1 or N1 amplitude in the present study. In sharp contrast, both components were influenced by emotional expression. This pattern of data is fully consistent with previous gaze-cuing studies using ERPs and manipulating also emotional expressions (Fichtenholtz et al., 2007, 2009). One possibility to account for the null amplitude modulation is that emotional expression may be a more important signal than eye gaze, characterized by a higher attentional priority. Future studies will possibly address this hypothesis directly and in more detail.

An increased amplitude in N2pc for spatially incongruent trials has recently been reported in a study assessing inhibition of return (McDonald, Hickey, Green, & Whitman, 2008). In that study, N2pc amplitude was lower when a target appeared at a recently attended location (i.e., spatially congruent trials) than when it appeared at a recently unattended location (i.e., spatially incongruent trials). However, the functional significance of the N2pc modulation with reference to inhibition of return is very different with respect to the context examined in the present study. Indeed, the larger N2pc on spatially incongruent over spatially congruent trials reported by McDonald et al. (2008) reflects the decreased likelihood of shifting attention from the fixation point towards a previously attended location due to inhibition of return. By contrast, in the present context, this very same pattern reflects the reorienting of attention from the distractor location towards the target location resulting from a previous

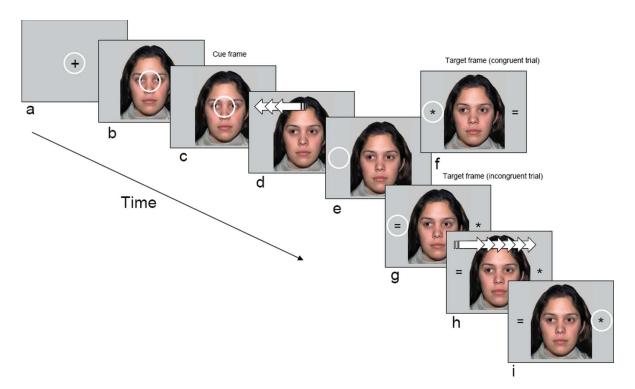


Figure 4. An illustration of the hypothetical attention dynamics as a function of events sequence occurring both on a spatially congruent and on a spatially incongruent trial. In this illustration, the "*" symbol acts as target stimulus, whereas the "=" symbol acts as distractor stimulus. Stimuli are not drawn to scale. White circles indicate holding of attention to a given location. White arrows indicate attention shifts. Participants are instructed to maintain fixation, and the attentional focus is likely aligned with the center of the screen when the face with straight gaze is shown (frames a and b). When the gaze of the model face becomes averted leftwards, attention is shifted according to the same directional vector, and then held on the left hemifield (frames c and d). When the target is shown, during spatially congruent trials, attention is located correctly (frame f). In spatially incongruent trials, however, attention is located in the wrong hemifield (frame g), and has to be shifted and reoriented to the correct target location (frames h and i).

shift of attention induced by reflexive gaze cuing. Correlational analyses between behavioral data and N2pc amplitude showed that a larger N2pc effect (i.e., a larger N2pc for spatially incongruent trials than for spatially congruent trials) was positively correlated to a larger gaze-cuing effect in accuracy measures. This pattern supports our argument that N2pc amplitude is related to attention shifts in gaze cuing, suggesting that amplitude differences that contribute to gaze cuing (at least in percentage of correct responses) reflect attention-shifting dynamics.

As regards the second aim of the study, the N2pc effect did not reveal modulations as a function of emotional expression of the face that were consistent with our expectations. In particular, we hypothesized that viewing an averted gaze may boost the likelihood of attention shifting in the corresponding direction when embedded in a fearful face, and reduce this phenomenon when embedded in a disgusted face. N2pc data basically mirrored the null influence of emotional expression on gaze cuing that emerged in behavioral data. One may argue that no such effects emerged in the present data because emotions

displayed by the specific faces used in the experiment were not particularly strong. However, the fact that emotional expression was overall effective in modulating electrophysiological measures at the level of both the P1 and N1 components renders it unlikely that our stimuli were not salient enough, and is, at least partially, consistent with recent views that emotion and attention are reflected in independent effects on cortical dynamics (Vuilleumier & Driver, 2007). As regards the effects of emotional expression, our data showed that targets appearing in the right visual field elicited an N2pc that was attenuated for fearful faces compared to both disgusted and neutral faces. Because this pattern was independent of cue-target congruency and was not expected, we can only speculate that the weaker N2pc may result from a mismatch between the hemisphere, which is assumed to be most involved in processing highly activating fear- and avoidance-related stimuli (i.e., the right hemisphere; see, e.g., Davidson, Ekman, Saron, Senulis, & Friesen, 1990) and the left hemisphere, which is at work processing targets appearing in the right visual hemifield. As regards specific ERP modulations as a function of emotional expression, these observed at the level of both the P1 and N1 in targetlocked analysis and at the level of the N170 in cuelocked analysis. In particular, the N170 elicited by cue onset was attenuated for disgusted faces compared to both fearful and neutral faces. The results of ERPs time-locked to target onset showed that the P1 was modulated by fearful faces, which were associated to a lower P1 with respect to both disgusted and neutral faces. In contrast, N1 amplitude was significantly smaller for neutral faces compared to both fearful and disgusted faces. Future work including other emotional expressions will test the robustness of the observed patterns and whether these amplitude modulations are sensitive to the prevalence of negative emotional expressions.

Overall, our data are consistent with recent studies that failed to find evidence for differential modulations of gaze cuing as a function of the emotional expression of the face. Fichtenholtz et al. (2007) provided evidence that for fearful and not happy faces, P3 response elicited by spatially incongruent targets was magnified with respect to spatially congruent targets. This was the only significant modulation of ERPs involving both emotion and attention. However, in a subsequent study in which fearful faces were compared to neutral faces, Fichtenholtz et al. (2009) failed to replicate this pattern. As argued above, no effects were reported in early ERP components (i.e., P1 and N1) time-locked to target onset in either study. The present research extended the findings of Fichtenholtz et al. (2007, 2009) and showed that emotional expression of the faces does not influence gaze cuing even when a novel and reliable index of attention shifting such as N2pc is considered. Our results are also consistent with a recent study by Holmes et al. (2010), who examined the effects of emotional expressions on gaze cuing by focusing on cue-locked ERP components. In agreement with Hietanen et al. (2008), their data revealed no hint of any EDAN modulation in gaze cuing. In contrast, gaze cuing was reflected in an amplitude modulation of the so-called anterior directing attention negativity (ADAN; see Nobre, Sebestyen, & Miniussi, 2000) occurring between 300 and 500 ms after gaze-cue onset. Holmes et al. (2010) interpreted this pattern as the neural underpinning of the mechanisms involved in holding attention at gazed-at locations. Most important, however, such ADAN modulation was independent of the emotional expression of the faces, which is consistent with the present findings as well as those reported by Fichtenholtz et al. (2009) concerning ERP components time-locked to target onset. Because we have

used a very brief SOA (200 ms), it was impossible for us to look for EDAN and or ADAN effects (if any), in our data set. Nonetheless, cue-locked analyses were performed to check the possible combined impact of both gaze and emotional expression prior to target onset. To this purpose, we focused on the face-sensitive N170 component (e.g., Bentin et al., 1996), which is also known to be sensitive to apparent motion of the eyes (e.g., Puce et al., 2000). The analysis showed that gaze direction and emotional expression exerted independent influences, in line with target-locked analyses. This pattern rules out the possibility that interactions between attention and emotion could be found early after gaze-cue onset, and is again in line with the findings reported by Holmes et al. (2010).

As regards the possible reasons for why no interactions between gaze cuing and facial expression were observed in the present results, it has recently been shown that the effects of social variables on gaze cuing are strongly context-dependent (Pavan, Galfano, & Castelli, 2010). In addition, Pecchinenda et al. (2008) tested several emotional expressions (fearful, disgusted, happy, and neutral faces) and provided evidence suggesting that the observation of interactive effects of gaze cuing and facial expression may depend, at least in part, on whether emotional processing is made task-relevant (also see Bayliss et al., 2007).

As a final consideration, it remains possible that ERP investigations are less than ideal for efficiently capturing areas relying on cortical regions specialized for processing disgust (e.g., Wicker et al., 2003) and subcortical circuits involving amygdala, which are known to mediate fear processing (e.g., Adams, Gordon, Baird, Ambady, & Kleck, 2003), in which interactive effects of emotion and attention may be more evident.

In conclusion, the results of the present study provide novel evidence showing that attentional dynamics in gaze cuing can be reflected in N2pc. Specifically, N2pc can be used as a marker for mapping attention shifts over space. Future studies will address the issue of whether the present results extend over different cue types that have been shown to elicit spatial shifts of attention even when task-irrelevant, such as arrows (e.g., Eimer, 1997; Tipples, 2002), numbers (e.g., Fischer, Castel, Dodd, & Pratt, 2003; Galfano, Rusconi, & Umiltà, 2006), body shadows (Galfano & Pavani, 2005; Pavani & Galfano, 2007), and direction words (e.g., Hommel, Pratt, Colzato, & Godijn, 2001).

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