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Effect of perceived eye gaze on the N170 component – A systematic review

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ABSTRACT

Direction of another person's eye gaze provides crucial information about their attention and intentions, which is essential for an effective social interaction. Event-related potential (ERP) measures offer precise temporal tracking of neural processes related to gaze perception. While the sensitivity of the ERP component N170 to face processing is principally agreed, the research on gaze direction effect on this component is thus far inconsistent. Here, we systematically reviewed literature on the sensitivity of N170 to gaze direction. We analysed if four factors, known to affect the face N170 (i.e., emotion, face orientation, task demand, and stimuli motion), were modulated by gaze direction. N170 sensitivity to gaze was reported the most in the studies that involved deviated faces, dynamic stimuli, and that used explicit tasks directly related to gaze or face processing. The present review provides a much-needed summary of the literature to date, highlighting the complexity of the effect of gaze direction on the N170 component, and the need of systematic studies investigating the combination of these factors.

1. Introduction

Eyes are one of the key elements of the human face playing a crucial role in everyday interactions. The eye region is the most attended feature of the face (e.g. Henderson et al., 2005), which makes it a prominent element in conveying information necessary for recognizing familiar faces (Lewis and Edmonds, 2003), discriminating gender (Schyns et al., 2002) and identifying emotions (Smith et al., 2005). Understanding others' gaze direction is a critical ability for social interaction, allowing us to perceive other people's intentions, and to identify another's direction of attention, be it towards oneself or any point in the environment. In humans the perception of gaze direction is associated with more complex and social functions, such as gaze following and joint attention (Emery, 2000), with the perception of others' gaze activating human motion-sensitive brain areas (Guterstam et al., 2020; Guterstam and Graziano, 2020a, 2020b). Although direct gaze is often perceived as a sign of dominance or even threat in non-human primates and some non-primate species (Emery, 2000), in

humans it has a central function of engagement of social communication. Direct gaze in humans, among other gaze directions, has a specific relevance for social interaction, which signals that someone is looking at, or attending to, the observer. Perception of direct gaze is thus used to regulate social interaction between people, to share intimacy and to exert social control (for a review see Kleinke, 1986). Preference for faces with direct gaze compared to averted was revealed to be present from the first days of life (Farroni et al., 2002), and preferential orienting to direct gaze manifests throughout early development (Farroni et al., 2007; Smith et al., 2006). Moreover, from early childhood, faces with direct gaze are encoded and recognised better than faces with averted gaze (Hood et al., 2003; Farroni et al., 2007). Atypical eye contact is among the diagnostic features in developmental disorders such as autism spectrum disorder (American Psychiatric Association, 2013; Senju and Johnson, 2009), which also highlights the crucial role of the perception of gaze direction on the development of neurotypical social behaviour.

Given the early emerging preference humans seem to have for direct

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gaze, as well as its importance for the development of social cognition, it is not surprising that gaze perception can have modulatory effects in a myriad of cognitive and social functions. For instance, perception of direct gaze has been shown to have an effect on the perception of the self and others (for a developmental review see Reddy, 2003), on public self-awareness (Pönkänen et al., 2011), emotional self-awareness (Baltazar et al., 2014), pro-social behaviour (Burnham and Hare, 2007; Manesi et al., 2016; Oda et al., 2011), and imitative behaviours (de Klerk et al., 2018; Marsh et al., 2016; Wang and Hamilton, 2014; Wang et al., 2011a, 2011b).

At the perceptual and cognitive levels, the presence of direct gaze has been shown to modulate face perception in several tasks. Such tasks include gender discrimination (Macrae et al., 2002; but see Vuilleumier et al., 2005), emotional processing, where direct gaze enhances the perception of approach-oriented emotions, such as anger and joy (Adams Jr and Kleck, 2005; Sander et al., 2007), evaluation of attractiveness, with faces with direct gaze being considered more attractive (Ewing et al., 2010) and, most notably, face recognition, whereby direct gaze seems to facilitate the recognition of face identity (Conty and Grèzes, 2012; Farroni et al., 2007; Mason et al., 2004; Smith et al., 2006; Hood et al., 2003).

Given the substantial modulatory role that eye gaze has on a wide range of social cognition, it is crucial to identify the neural mechanisms underlying its perception, as well as its influence on other cognitive processes. Electroencephalography (EEG) provides us with direct measures of summative field potentials generated in the brain with a very high temporal resolution, and thus can help understand the neural mechanisms underlying the processing of gaze-direction. Numerous studies have indeed shown that gaze direction differentially modulates the electrophysiological responses associated with face processing. Studies focusing on event-related potentials (ERPs) evoked by gaze direction usually explore specific ERP components, such as the P100, the N170 or the P350 (e.g., Burra et al., 2018; Nomi et al., 2013; Puce et al., 2000), with few studies analysing a larger time period after stimulus onset (Itier et al., 2007; Klucharev and Sams, 2004; Yokoyama et al., 2013).

Among the different ERP components, the N170 is the most commonly reported in studies investigating gaze processing - which might not be surprising given its prevalence as the most broadly studied ERP marker of face processing. The N170 is generally described as a face-sensitive component (Bentin et al., 1996), and is characterized by a negative peak occurring around 170 ms after stimulus onset in lateral temporo-occipital areas (for reviews on the N170 component see Eimer, 2011; Rossion and Jacques, 2012). In the broader context of electrophysiological studies on face processing, numerous studies have confirmed that the N170 consistently displays an increased negative amplitude to faces as compared to non-face objects (Bentin et al., 1996). Hence, the N170 has been considered an electrophysiological marker of face processing. It has been suggested that this component reflects the perceptual structural encoding of faces, which has been associated to its well-known modulation by face inversion (i.e. larger N170 amplitudes for inverted faces as opposed to upright faces). Consequently, the increased N170 for inverted faces has been proposed to be associated with an additional recruitment of eye-sensitive cells which would instead be inhibited when the eyes are presented in the context of an upright face (Itier et al., 2007). The sensitivity of this component to the eye region even when presented in isolation (Bentin et al., 1996) makes it particularly well suited to study gaze processing in the human brain. Multiple studies to date have reported a larger N170 for eyes presented in isolation as compared to all other facial features (Bentin et al., 1996; Taylor et al., 2001; Nemrodov et al., 2014; but see Parkington and Itier, 2018) or even compared to whole faces (e.g., Bentin et al., 1996; Itier et al., 2006). These findings have led to the hypothesis that the N170 is partially a marker of a neural eye detector (Nemrodov et al., 2014). In line with this, the N170 component shows a different developmental trajectory for perception of the eye region compared to the overall face

(Taylor et al., 2001). While the N170 amplitude evoked by the eye region matures early in childhood, stabilising around 11 years of age, a later development of this component is observed for the presentation of the whole face, which continues to mature until adulthood (Taylor, Edmonds et al., 2001). Accordingly, the role of the eye region perception on the N170 morphology could be one of the driving factors for researchers to investigate whether the N170 is also sensitive to the direction of gaze itself.

Findings to date suggest that potential effects of gaze direction on the N170 component are very complex in nature as evidenced by the mixed results found in the literature. On one hand, several studies have failed to find any differences between direct and averted gaze (Grice et al., 2005; Klucharev and Sams, 2004; Pönkänen et al., 2011; Taylor, Itier et al., 2001; Yokoyama et al., 2013). On the other hand, even within studies that find differences between gaze directions, results are not consistent, whereby some report larger N170 amplitudes for faces with direct gaze (e.g., Conty et al., 2007; Pönkänen et al., 2011), while others reveal larger N170 amplitudes for faces with averted gaze (e.g., Itier, Alain et al., 2007; Puce et al., 2000). A possible interpretation of these inconsistent findings is that gaze processing is modulated by several factors related both to bottom-up differences in the stimuli and top-down differences in context and task-demand, which have not been systematically manipulated across different studies. Thus, it is critical to systematically evaluate the studies analysing the existence of an effect of gaze direction on the N170 component in order to identify potential modulating factors.

Here we conducted a systematic review of all studies that have analysed the sensitivity of the N170 component to gaze direction. Furthermore, this review seeks to highlight the complexity of gaze processing as measured with N170 component, and the possible modulatory role of different factors such as facial expression of emotion, face orientation, task demand and the motion of the stimuli. Given the large variability of manipulations of stimuli and tasks, and the lack of enough reports with similar manipulations that could be grouped, the systematic approach seems to us the most appropriate concerning the current status of literature addressing this specific topic.

2. Methods

2.1. Literature search and study selection

A systematic search was conducted on PubMed on the 12 of December 2021 using the terms: ("eye contact" OR "direct gaze" OR "eye gaze" OR "mutual gaze" OR "averted gaze" OR "looking toward" OR "forward gaze" OR "gaze direction") AND (ERP OR N170 OR EEG). Only peer-reviewed, English language publications with original research were included.

Studies were retained if they compared direct with averted eye gaze, using ERP measures, specifically focusing on the N170 component, in a neuro-typical adult sample. Gaze cueing and adaptation paradigms, as well as studies presenting more than one face simultaneously were excluded. Studies using intracranial recordings were also excluded. An extraction sheet was created containing: 1) the number of participants analysed, 2) the task participants performed, 3) face orientation (e.g. frontal or deviated face), 4) type of stimuli presented (e.g. live, photographic, schematic faces), 5) facial expression of emotion, 6) type of presentation (e.g. static, dynamic, live), 7) similarity of baseline (e.g. are participants observing the same stimuli in the baseline period for direct and averted gaze trials), 8) ERP components analysed, 9) N170 amplitudes and 10) latencies measurements, 11) electrodes analysed and 12) first significant difference between direct and averted gaze measured in the ERP waveform.

2.2. Data extraction

We first analysed the influence of four factors on the presence of an

effect of gaze direction on the N170 component (i.e., whether N170 amplitudes and/or latencies differed between direct and averted gaze). These factors were: 1) facial expression of emotions, 2) face orientation, 3) task, and 4) type of stimulus presentation (static, dynamic or live). We then analysed how these factors contributed to the directionality of this effect (e.g., whether the N170 component was larger for direct or averted gaze). Note that this last analysis only included studies in which the effect of gaze direction on the N170 was present, which restricted the number of studies to be included. Finally, to explore a potential modulation of perceived gaze direction in prior stages of visual processing, we present a brief discussion of the factors contributing to the effect of gaze direction on the P100 component.

3. Results

3.1. Literature search and study selection

Following the systematic search, 190 studies were identified and five references were included from external sources, making a total of 195 studies screened. Eighty-five full-text articles were assessed for eligibility based on titles and abstracts (Fig. 1), excluding all studies that clearly were not relevant to the topic or did not include EEG measurements (110 studies). Of those considered, 51 studies were excluded: 16 were removed for not analysing ERPs; 11 for not looking directly into the N170; 12 for not comparing direct and averted gaze; 8 because they did not test a neuro-typical adult sample; 2 for displaying more than one face simultaneously; 2 for using intracranial EEG, 1 for having a saccade contaminated N170 component, and 1 for using an adaptation paradigm. A total of 34 studies met inclusion criteria and are summarized in Table 1. Only data from neurotypical participants is discussed and summarized. Two studies were kept that did not explicitly analyse the N170 component: a) one referred to the N190 which was measured in temporal areas (Watanabe et al., 2002) and was described by the authors

as matching the N170 component analysed in other studies (two of these studies are included in this review: (Puce et al., 2000; Taylor, Itier et al., 2001); b) the other study analysed the whole waveform using 30 ms time bins, covering the N170 time-window in relevant temporo-parietal channels (Klucharev and Sams, 2004).

Several of the analysed studies contained more than one condition with one or more of the factors analysed (e.g., studies containing both frontal and deviated faces or neutral and emotional facial expressions).

3.2. Facial expression of emotion

Out of the 34 selected studies 9 presented emotional face expressions (e.g. anger, fear, happiness, see Table 1 for precise stimulus distribution) and the remaining 25 presented neutral faces. Out of 9 studies using emotional expressions, 6 found no effect of gaze direction on the N170 amplitude or latency (Klucharev and Sams, 2004; Li et al., 2017; Nomi et al., 2013; Rigato et al., 2010; Tso et al., 2015; McCrackin and Itier, 2019). One of the three studies that did reveal an effect, was using dynamic facial stimuli, whereby the gaze of neutral, happy or angry faces was shifting towards to or away from observer (Stephani et al., 2020). Emotional expression modulated the N170 amplitude with happy faces having larger amplitudes than angry faces, but there was no interaction between gaze direction and emotional expression. The remaining two studies (Conty et al., 2012; El Zein et al., 2015), shared a similar paradigm, in which three variables were manipulated: gaze direction (direct and averted), pointing (present or absent) and emotion (neutral and anger). Although in both studies there was a main effect of gaze (i.e., larger amplitudes for direct compared to averted gaze), only El Zein et al. (2015) found an interaction between gaze direction and emotion in the N170 component with larger amplitudes for faces with direct gaze and angry expressions compared to neutral. In Conty et al. (2012) study, interaction of gaze and anger cues appeared only at a later stage in the frontal P200 component. This is consistent with the majority of the

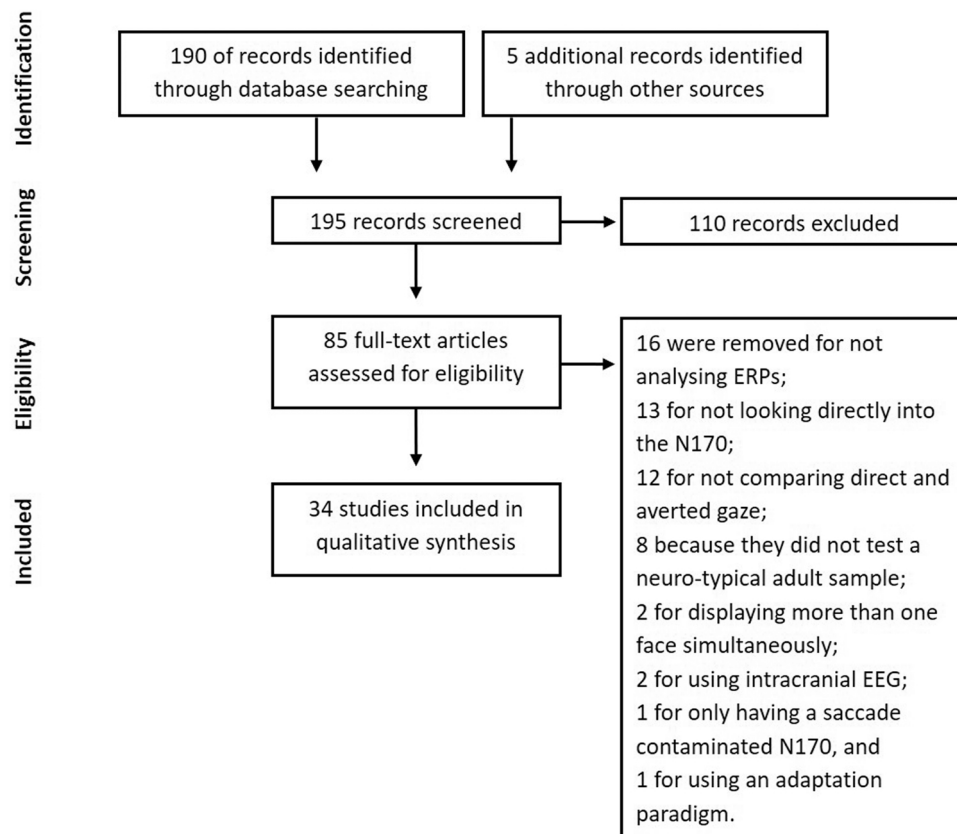


Fig. 1. Flowchart of the identification of studies, their screening, eligibility assessment and final inclusion.

Table 1
Table summarizing all analysed studies.

Study	N	Tasks	Face Orient.	Stimuli	Emotion	Presentation mode	Baseline	Components (time windows)	N170 Amplitude	N170 Lat	Electrodes analysed	1st dif (ms) or component
Puce et al. (2000)	20 ♂	Passive	Frontal	Faces and eyes (photo) Checkers	Neutral	Dynamic	Different (DG to AG vs AG to DG (exp 1 included open mouth to DG))	P100 N170 P350	AG > DG (in several posterior electrodes, in exp. 1 and P10 in exp. 2)	Earlier to AG than DG	Analysis per pair: C3/4, P3/4, T7/8, TP7/8, P7/8, PO7/8, O1/2, TP9/10, P9/10, PO9/P10	N170
Taylor et al. (2001)	27 (13 ♂)	Target detection	Frontal	Faces and eyes (photo)	Neutral	Static	Same	N170 VPP	ns	ns	P7, P8, P9 and P10	ns
Watanabe et al. (2002)	14 (8 ♂)	Passive	Frontal	Faces (photo) Chequered control	Neutral	Static	Same	N190 (N170 measured on T5' and T6'); P200	AG > DG	ns	Cz, T5' and T6'	N190
Kimura et al. (2004)	8 (4 ♂)	Target image count	Frontal	Faces (photo) and scrambled version	Neutral	Static	Same	P100 N170	ns	ns	T5 and T6	na
Klucharev and Sams (2004)	11 ♂	Search for same gaze direction across trials	Frontal	Faces (photo)	Happy, Angry	Static	Same	Whole wave	ns	na	30 channels across the scalp. Gaze differences in O1/2 and P8 and P10	85
Grice et al. (2005)	10	Passive	Frontal	Faces (photo)	Neutral	Static	Same	N170	ns	ns	L: 64, 65, 66, 69, 70, 74, M: 71, 75, 76, 82, 83, 84, and R: 85, 89, 90, 91, 95, 96	na
Conty et al. (2007)	14 (7 ♂)	Gaze judgement	Deviated and frontal	Faces (photo)	Neutral	Dynamic	Same (midpoint to AG or DG)	N170 P300	AG < DG both orientations, but more in deviated head orientation	Later DG than AG	electrodes among CP5/6, P5/6, PO1/2, TP7/8, P7/8, PO7/8, TP9/10, and PO9/10	N170
Itier et al. (2007)	16 (6♂)	Head and gaze direction	Deviated and frontal	Faces (photo)	Neutral	Static	Same	N170; PLS analysis of the whole epoch	AG > DG only when faces were in front-view	AG later than DG	N170 at P7/P8 and CB1/CB2	N170
Rigato et al. (2010)	13 (5♂)	Passive	Frontal	Faces (photo)	Neutral, Fear, Happy	Static	Same	P1 N170 P2 (several other timewindows)	ns	ns	OT sites for N170: 58, 59, 63, 64, 65, 66, 69, 70, 71 (L), 84, 85, 90, 91, 92, 95, 96, 97, 100 (R), 61, 67, 68, 72, 73, 77, 78, 79 (M)	P2 interacting with emotion
Pönkänen et al. (2011)	20 (4 ♂)	Passive	Frontal	Faces (Live and photos)	Neutral	Live or Static	Same	P1, N170, EPN	AG < DG -live stimuli; AG vs DG ns - static photos	na	O1/2, T5/6	N170
Conty et al. (2012)	21 (11♂)	Attention judgement (on participant or other); degree of perceived self-involvement	Frontal for DG deviated for AG	Faces (photo) including part of the torso and in some trials pointing	Neutral Angry	Dynamic	Same (midpoint to AG or DG)	P100 N170 P200	AG < DG	Later to DG than AG	For N170: P5/P7/CP5/TP7, P6/P8/CP6/TP8	P100
Doi and Shinohara (2012)	16 ♀	Open eyes detection (faces with closed eyes as distractors)	Frontal	Faces (photo): own or unfamiliar children	Neutral	Static	Same	P1, N170 and P3	AG < DG (own children); ns - unfamiliar children	ns	N170 at T5/T6	N170
Schmitz et al. (2012)	LSA: 25 (13♂) HSA: 26 (14♂)	Reporting the location of a probe (R or L) appearing after gaze presentation	Frontal	Eyes	Neutral	Static	Same	P1 N170 EPN LPP	ns	na	N170 at P7, P8	P100 (trend)
Nomi et al. (2013)	20 (11 ♂)	Target detection	Frontal	Faces (photo)	Happy, Neutral, Angry, Fear	Static	Same	30–80, P1, (N170, and 200–400 ms.	ns	na	T5/6, O1/2	200–400

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Table 1 (continued)

Study	N	Tasks	Face Orient.	Stimuli	Emotion	Presentation mode	Baseline	Components (time windows)	N170 Amplitude	N170 Lat	Electrodes analysed	1st dif (ms) or component
Rossi et al. (2014)	22 (11♂)	Colour change detection	Frontal	Schematic faces	Neutral	Dynamic	Different (DG to AG vs AG to DG)	N170 ERSP	ns	ns	9 electrodes, clusters centered on equivalent to P7 and P8	100 (ERSP)
Yokoyama et al. (2013)	12 (9♂)	Gaze judgement (CFS task)	Frontal	Faces (photo)	Neutral	Static	Same	N170; Whole wave (50 ms bins)	ns	na	O1, O2, T5, and T6	200
El Zein et al. (2015)	18 (8 ♂)	Expression task or gaze direction task	Frontal for DG and deviated for AG	Faces (photos) including part of the torso, and in some trials pointing	Neutral Angry	Dynamic	Same (midpoint to AG or DG)	P100 N170 P200 LPP	AG <DG; no interaction with task	na	For N170: P7/TP7/TP9, P8/TP8/TP10	N170
Myllyneva and Hietanen (2015)	19 (9 ♂)	Passive	Frontal	Live faces	Neutral	Live	Same	N170; early centro-parietal and lateral OT activity; P3	ns	na	N170 at PO8/7, P8/7 and P6/5	160–300
Latinus et al. (2015)	22 (11♂)	Social: gaze judgement (away or towards); non-social: motion judgement (to the R or L)	Frontal	Faces (photo)	Neutral	Dynamic; 1. DG to ext AG; 2. Ext AG to DG; 3. Int AG to ext AG; 4. 3 and 4 Int AG to DG; 5. DG to int AG; 6. Ext AG to int AG	1 and 2 different, 3 and 4 same, 5 and 6 different	N170; Spatiotemporal analysis	1 vs 2: non-soc: AG > DG; soc: ns in RH, AG > DG in LH; 3 vs 4: non-soc: AG > DG in RH, ns in LH; soc: ns in RH, AG > DG in LH; 5 vs 6: non-soc: AG > DG soc: ns in RH	1 vs 2 ns 3 vs 4 ns 5 vs 6 ns	Nine electrodes cluster on parieto-occipital sites centered around maximal N170 activation (LH and RH)	106 ms (Spatiotemporal analysis)
Rossi et al. (2015)	16 (7♂)	Target detection	Frontal	Faces (schematic and photo); scrambled versions	Neutral	Dynamic	Different (DG to AG vs AG to DG)	N170 ERSP analysis	AG > DG (Photo) ns for schematic	ns	9 OT electrodes including equivalent to P07/8 and P9/10	150 ms in ERSP
Tso et al. (2015)	32	Gaze judgement (away or towards participant); threat rating	Deviated and frontal	Faces (photo);	Neutral Fear	Static	Same	N170	ns	ns	P7 and P8	N170
Tye et al. (2015)	13 (11♂)	Target image count	Frontal	Upright and inverted faces (photo)	Neutral	Static	Same	P1 N170	ns	ns	L: 58, 59, 64, 65, 66, 68, 69, 73; R: 84, 88, 89, 90, 91, 94, 95, 96.	na
Berchio et al. (2016)	14 (9 ♂)	2-back face recognition	Frontal	Faces (photo)	Neutral	Static	Same	P100 N170 P200 (all time points) P100 N170, DISS and Topographic analysis based on micro-state segmentation	AG <DG	na	All electrodes	50 ms
Burra et al. (2016)	15 (7 ♂)	Gender judgement	Frontal	Faces (avatars) with broad, low or high spatial frequency information	Neutral	Static	Same	Same	AG > DG	ns	L and R OT clusters	Around 40 (topographic analysis)
Burra et al. (2017)	13 (10♂)	Gender judgement	Deviated and Frontal	Faces (photo)	Neutral	Static	Same	P100, N170, Global Field Power analysis	AG <DG	ns	For N170 an electrode was chosen amongst TP9/10, P9/10, PO9/10, O9/10 where this component was maximal per condition and participant	N170 for ERPs (EEG)
Li et al. (2017)	HSA, (23,9♂); LSA, (23,10♂)	Gender judgement	Frontal	Faces (photo)	Anger vs Neutral	Static	Same	P1 N170 N2	ns	ns	For N170: P7 and P8	P1
Tsuji and Shimada (2017)	HSA (8; 4 ♂) LSA (8; 4 ♂)	Passive	Frontal	Eyes (photo) in DG, AG and closed eyes	Neutral	Static	Same	N170 P2	ns	ns	N170 at P8	P2 latency in a highly socially anxious group
Burra et al. (2018)	20 (11 ♂)	Gender judgement	Frontal	Faces (photo)	Neutral	Static	Same	P1 N170 P3a P3b	ns	ns	For N170: P7, Po8, P7, P8, P9, P10	P100

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Table 1 (continued)

Study	N	Tasks	Face Orient.	Stimuli	Emotion	Presentation mode	Baseline	Components (time windows)	N170 Amplitude	N170 Lat	Electrodes analysed	1st dif (ms) or component
Mares, Smith et al., (2018)	15 (5 ♂)	Target detection	Deviated	Faces (photo)	Neutral	Dynamic	Same	P1 N170 N240	AG < DG	na	TP7/8, P7/8, PO7/8	N170
McCrackin and Itier (2018)	56 (29 ♂)	1) Self or other relevance sentence reading; 2) rating of positive or negative feelings elicited by a face; 3) rating of level of arousal elicited by a face.	Frontal	Faces (photo)	Neutral	Static	Same	N170 and 50–150 ms, 150–250 ms, 250–350 ms, 350–450 ms, 450–550 ms, 550–650 ms time windows	AG > DG for positive self-relevant trials	ns	Maximal electrode amongst PO7/8, P9/10 TP9/10, PO9/10 and O1/2	N170
McCrackin and Itier (2019)	26 (9 ♂)	a) Gaze direction judgement; b) gender judgement; c) discrimination of facial emotion.	Frontal	Faces (photo)	Angry and happy	Static	Same	N170: 130–200 ms; Frontal: 200–400 ms; Parieto-occipital: 200–500 ms	ns	ns	For N170: P9, P10, PO9, PO10, P7, P8.	Around 220 ms
Stephani et al. (2020)	21 (9 ♂)	Counting of gaze shifts in the sequence during: a) Active viewing (fixate the mouth, then shift the gaze to the L or R eye; b) Passive viewing.	Frontal	Faces (photo)	Neutral, angry and happy	Dynamic Gaze changes occur: a) once participant shifts her/his gaze; b) at random interval.	Same	N170: 130–220 ms. EPN: 200–400 ms. P300: 150–400 ms	DG to AG (away from observer) > AG to DG (towards the observer)	ns	For N170: PO8	N170
McCrackin and Itier (2021a)	44 (21 ♂)	1) Reading sentences describing positive, negative or neutral events; 2) viewing faces of individuals to whom this event occurred; 3) empathy and emotional valence ratings.	Frontal	Faces (photo)	Neutral	Static	Same	Exploratory analyses at 50–800 ms; N100: 50–120 ms; N170: 130–200 ms; N200: 200–350 ms; EPN: 200–500 ms	AG > DG	ns	For N170: P9, P10, PO9, PO10, P7, P8.	N100
McCrackin and Itier (2021b)	44 (21 ♂)	1) Reading sentences describing positive, negative or neutral events; 2) viewing faces of individuals to whom this event occurred; 3) ToM rating of how the presented person is feeling.	Frontal	Faces (photo)	Neutral	Static	Same	Exploratory analyses at 50–800 ms; N100: 50–120 ms; N170: 130–200 ms; N200: 200–350 ms; EPN: 200–500 ms	ns	ns	For N170: P9, P10, PO9, PO10, P7, P8.	N100

Abbreviations: AG, averted gaze; CFS, continuous flash suppression; DG, direct gaze; DISS, global topographic dissimilarity; ERSP, Event related spectral perturbation; exp., experiment; Ext, extreme; HSA, high social anxiety; Int, Intermediate; L, Left; LH, left hemisphere; LSA, low social anxiety; M, Medial; na, non-applicable; ns, non-significant; OT, Occipito-temporal; PLS, Partial Least Square; R, Right; RH, right hemisphere; ToM, Theory of Mind; VPP, vertex positive potential.

studies showing a later integration of gaze and emotion cues, occurring after the N170 component, around 200 ms after stimuli display. Specifically, Nomi et al. (2013) found an integration of gaze and emotion between 200 and 400 ms, Klucharev and Sams (2004) - between 270 and 330 ms, and Rigato et al. (2010) - in the P2 component (around 240 ms).

Based on the reviewed studies, presence or absence of facial expression of emotion does not seem to play a systematic role in modulating gaze effects on the N170.

3.3. Face orientation

Studies using front view faces found mixed results, with 14 out of 28 studies reporting an effect of gaze, out of which 7 found larger amplitudes for averted gaze. Studies using deviated faces yielded more consistent results, with 5 out of 7 studies reporting an effect of gaze. It suggests that head orientation can have an effect on the perception of gaze at the level of the N170 component. It has been argued that the use of deviated faces might lead to an enhanced gaze encoding (Latinus et al., 2015), which is corroborated with the observation that larger effects of perceived direct gaze on the N170 component were found for deviated faces compared to frontal (Conty et al., 2007). Moreover, in all studies, where an effect of gaze was observed for deviated faces, the direction of the effect was also consistent: N170 amplitudes were larger for direct compared to averted gaze (Burra et al., 2017; Conty et al., 2012, 2007; El Zein et al., 2015; Mares et al., 2018; Pönkänen et al., 2011). Of note, two of the studies that showed effects of gaze direction (Conty et al., 2012; El Zein et al., 2015) always displayed front view faces with direct gaze and deviated faces with averted gaze, not allowing for a clear distinction between effects of gaze and head orientation on the N170.

In summary, the above reviewed studies indicate that head orientation modulates the gaze direction effect on N170 component, so that faces with direct gaze presented in deviated orientation induce larger N170 amplitudes. The precise underlying mechanism is still not clear, but it is consistent with a claim that perception of gaze direction can be modulated by head orientation (Langton et al., 2000), which, in turn, could lead to the need of a deeper gaze encoding to deal with the combination of head and gaze cues. It is likely that the incongruence between head and gaze direction result in a better gaze discrimination, mainly due to the larger visibility of the white sclera.

3.4. Task

The tasks used in the analysed studies were divided into three categories, a) tasks that were specific to eye/gaze processing (11 studies); b) tasks that required face processing for which processing of the eye region is relevant (11 studies); c) tasks that were irrelevant to face or gaze processing, or where participants were asked to passively attend to the stimuli (15 studies). Tasks considered as gaze-related included tasks of gaze discrimination (Conty et al., 2007; Itier et al., 2007; Tso et al., 2015; Yokoyama et al., 2013; McCrackin and Itier, 2019), detection of same gaze direction across trials (Klucharev and Sams, 2004), gaze change counting (Stephani et al., 2020), detection of open eyes (Doi and Shinohara, 2012), eye motion to the right or left (Latinus et al., 2015), and judgement of stimuli attention on self or other (Conty et al., 2012; El Zein et al., 2015; Latinus et al., 2015). Several tasks were considered as requiring face processing, namely judgement of facial expression (El Zein et al., 2015; McCrackin and Itier, 2019), head direction (Itier, Alain et al., 2007), face recognition (Berchio et al., 2016), gender categorization (Burra et al., 2016, 2017, 2018; Li et al., 2017; McCrackin and Itier, 2019), rating of a face affective and arousal impact on self (McCrackin and Itier, 2018), empathy and emotional valence ratings to previously presented faces described in a context (McCrackin and Itier, 2021a), and theory of mind judgements about faces previously described to encounter positive, neutral or negative scenarios (McCrackin and Itier, 2021b). Finally, we considered tasks irrelevant to

face or gaze processing as the following: target counting (Kimura et al., 2004; Tye et al., 2015), colour change identification (Rossi et al., 2014), target detection (Mares et al., 2018; Nomi et al., 2013; Rossi et al., 2015; Taylor, Itier et al., 2001), and probe localization (Schmitz et al., 2012).

When the task was specific to eye/gaze processing, gaze direction affected N170 amplitudes in 7 out of 11 studies. The same pattern was also observed in tasks that required face processing where the eye region was relevant for the task at hand, in which N170 amplitudes differentiated gaze direction in 7 out of 11 studies. By contrast, when using other unrelated or passive tasks, the majority of studies did not find an effect of gaze direction on N170 amplitudes (10 out of 15 studies). Looking at the remaining five studies that did find significant effects, four of them used dynamic or live stimulus presentation (Mares et al., 2018; Pönkänen et al., 2011; Puce et al., 2000; Rossi et al., 2015), and, indeed, in one of them (Pönkänen et al., 2011) the effects of gaze direction were only observed for live but not static stimuli, which will be discussed in the next section.

Taken together, task demands appear to modulate gaze processing, which, in turn, suggests that gaze perception is affected by top-down processes. In addition to tasks explicitly requiring eyes or gaze processing, face processing tasks could also be associated with a deeper encoding of the eye region (El Zein et al., 2015). Indeed, the eye region has been shown to contain important information for face detection (Burton and Bindemann, 2009; Lewis and Edmonds, 2003), identity (Caldara et al., 2005; McKelvie, 1976; Schyns et al., 2002), gender (Schyns et al., 2002) and facial expression (Calder et al., 2000; Smith et al., 2005).

3.5. Dynamic or live stimuli

Out of 24 studies that employed static images of faces, 16 found no difference between gaze directions. By contrast, out of 11 studies that used either live or dynamic faces, 8 found differences between gaze directions. Moreover, in one of the studies which employed both live and static photos of faces, N170 amplitudes were modulated by gaze direction only when live faces were used (Pönkänen et al., 2011). Additionally, one of the two studies that used dynamic stimuli and did not find an effect, used schematic faces (Rossi et al., 2014), which did not have the typical local contrasts associated with gaze perception. A further study also supported this interpretation, by showing that N170 amplitude modulation for different gaze direction was observed in real faces but not in schematic stimuli (Rossi et al., 2015).

Taken together, the outcomes of the reviewed studies strongly suggest that N170 sensitivity to gaze direction is most prominent when the participants observed dynamic gaze shifts or live stimuli.

3.6. Relevant factors for the directionality of gaze effects on the N170

In the previous four sections, we analysed the influence of four factors on the presence of the effect of gaze direction on N170 (i.e., whether N170 amplitudes differed between direct and averted gaze). In this section, we consider the directionality of the effect of gaze direction on the N170 (i.e., whether N170 amplitudes were larger for direct or averted gaze).

The results reveal that the effect of gaze direction on the N170 component comes with mixed directionality, that might depend on several factors. Of the 16 studies where an effect of gaze was present, 8 found larger amplitudes for direct gaze and 8 for averted gaze. Of relevance, face orientation seems to play an important role, whereby all studies that found a larger N170 amplitude for averted gaze used frontal faces as stimuli, and the majority of studies (5 of 8) that found an enhanced N170 for direct gaze included deviated faces as stimuli. Conversely, in all the studies in which the effect of gaze direction was present AND deviated faces were used as stimuli, the directionality of the effect was the same: N170 amplitude was larger for direct gaze.

This trend seems to be most prominent when dynamic stimuli were

used: all studies using dynamic frontal faces found a larger N170 for averted gaze, while studies including a deviated head orientation, found larger N170 amplitudes for direct gaze. Note that [Itier, Alain et al. \(2007\)](#) found larger amplitudes for averted gaze in frontal faces that disappeared with deviated faces. However, this does not seem to be due to an overall increased amplitude for incongruent head and gaze directions, since both [Conty et al. \(2007\)](#) and [Burra et al. \(2017\)](#) found increased N170 amplitudes for direct gaze when frontal and deviated faces were intermixed during stimulus presentation. Furthermore, two other studies found an overall increased amplitude for direct gaze using congruent gaze and head orientations ([Conty et al., 2012](#); [El Zein et al., 2015](#)). Together, these studies suggest that increased N170 amplitudes for direct gaze are more likely to be observed when deeper gaze encoding is needed due to the presence of incongruence between head and eye directions within the stimulus array, which might have a carryover effect on trials with front view faces.

By contrast, we did not find a consistent pattern on the effect of emotion or task on the directionality of the effect of gaze direction on N170.

3.7. P100

In this final section, we present a small exploratory analysis on the P100, which is out of the scope of our systematic review, to explore a possible influence of gaze direction on the earlier stage of visual processing. Of all the papers analysed, 15 of them looked into this component. Nonetheless, only 5 of them found an effect of gaze, all showing larger P100 amplitudes for averted gaze compared to direct ([Berchio et al., 2016](#); [Conty et al., 2012](#); [Li et al., 2017](#); [Schmitz et al., 2012](#); [Burra et al., 2018](#)). The majority of these studies used static stimuli and frontal faces ([Berchio et al., 2016](#); [Burra et al., 2018](#); [Li et al., 2017](#); [Schmitz et al., 2012](#)), with one exception ([Conty et al., 2012](#)), in which both frontal and deviated faces were presented dynamically. No clear pattern was found for the tasks employed, with these studies using tasks that required face ([Berchio et al., 2016](#); [Li et al., 2017](#); [Burra et al., 2018](#)), gaze processing ([Conty et al., 2012](#); [Burra et al., 2018](#)) or neither. Furthermore, no interaction with emotion was observed, despite two studies including angry expressions ([Conty et al., 2012](#); [Li et al., 2017](#)). Taken together, these findings suggest that the P100 has limited sensitivity to gaze direction.

4. Discussion

While the N170 component is well characterized for its face sensitivity ([Bentin et al., 1996](#)), and its sensitivity to the eye region in particular ([Bentin et al., 1996](#); [Nemrodov et al., 2014](#); [Taylor, Itier et al., 2001](#)), its role in processing gaze direction is less understood. Our review has highlighted that potential effects of gaze direction on the N170 amplitudes are highly sensitive to the task demand and the properties of the stimuli, suggesting that they derive from a complex combination of top-down control and/or contextual modulation. Findings combined from the studies reviewed do not show a consistent pattern on how gaze processing affects the N170 component. This is most likely due to widely different combination of methodologies used in these studies, leading to the inconsistencies observed in their results. To the best of our knowledge, we are the first to report a systematic review that has analysed the sensitivity of this well-known ERP component to gaze direction.

A few consistent patterns have emerged from the review. Overall, N170 sensitivity to gaze direction seems to be associated with conditions where a deeper processing of gaze direction is needed either to a) accomplish a task, such as an explicit gaze related task, or a more general face processing task; to b) deal with possible incongruences between head and gaze orientations; or to c) process dynamic shifts of gaze or live gaze presentation. Moreover, there is an evident split in the directionality of the effect of gaze direction on the N170 component, with around half of the studies showing an increased amplitude for direct gaze and

the other half for averted gaze. A particularly relevant factor for the directionality of the effects of gaze seems to be head orientation, with the presence of deviated faces in the stimulus sequence being more likely to result in enhanced N170 amplitudes for direct gaze, often extending to trials with frontal faces in the stimulus sequence.

The mechanisms underlying the influence of deeper gaze/face encoding on N170 modulation are not yet clear, but several relevant theories have been proposed. Firstly, increased self-relevance has been suggested to play a role (but see [McCrackin and Itier, 2018](#)), where cues that promote it (e.g., direct gaze, pointing towards, and approach oriented emotions) are associated with larger N170 amplitudes ([Conty et al., 2012](#); [El Zein et al., 2015](#)) possibly having an additive effect. In line with this, [Doi and Shinohara \(2012\)](#) found larger N170 amplitudes for direct gaze only when mothers were observing photographs of their own children, in the absence of any gaze effect when observing photographs of unfamiliar children. Secondly, arousal elicited by the perception of eye contact has also been proposed to play a role in gaze related N170 activity ([Hietanen, 2018](#)). Supporting this hypothesis, an increased N170 component, together with increased arousal ratings has been found for direct gaze compared to averted for live but not static faces ([Pönkänen et al., 2011](#)). Studies, analysing skin conductance responses as a measure of arousal, support this perspective showing increased arousal for direct gaze in comparison to averted ([Helminen et al., 2011](#); [Hietanen et al., 2008](#)).

Finally, the impact of gaze direction on other ERP components, besides the N170, requires future attention. For example, recent data revealed that the P1 component was sensitive to gaze direction AND task-demand, i.e., larger P1 for direct as compared to averted gaze or closed eyes required a strong face encoding, while this difference was absent when such encoding was not mandatory ([Burra et al., 2018](#)). Such evidence highlights the role of task-demand on early modulations of electrophysiological markers as well as its impact at an early stage of visual processing, even prior to the N170 component. Further experiments are required to disentangle the role of tasks and context in the early coding (P1 or even earlier) of gaze direction.

In this systematic review we covered four experimental factors which are most commonly manipulated in the electrophysiological studies on gaze direction. Future studies will be required to examine other factors crucial for ERP analysis, such as the pre-processing of electrophysiological data. For example, previous studies have varied in different methodological factors such as the filtering of the raw EEG data (low-cut off or high-cut off parameters) or its nature (see [Acunzo et al., 2012](#) for such discussion regarding facial expressions' ERPs), the selection of electrodes of interest to measure the N170, as well as the reference (for the implication of these factors on N170 see [Rossion and Jacques, 2008](#)), the type of electroencephalographic analysis performed (mean amplitudes, peak-analysis, global field power measures, etc.), the application of a blink artefact correction on the raw EEG signal, or the possible discarding of trials including saccades. As these factors substantially affect the results on N170 modulations by gaze direction, we highlight the importance of the inclusion of all these parameters in reports, as recommended by the guidelines of [Picton et al. \(2000\)](#), so that future studies could systematically analyse the impact of these methodological factors. We would also encourage trying to apply robust methodological techniques (see, for example, [McCrackin and Itier, 2021a, 2021b](#)) that not only allow to distinguish differences in amplitudes but also to very precisely track the time course, shifts and interactions of different ERP components. In the same vein, the precision and definition of gaze processing effects could be enhanced with the ERP decoding technique (see for example [Bae, 2021](#)) allowing to detect, at which given time point the pattern of neural activity of a certain condition is distinguishable from the other condition. For the reason that such measures could not be performed on the conventional ERP analyses level, ERP decoding approach could improve the precision of the outcome effects and hence, the interpretation of results.

The systematic review provided in this paper clearly shows that the

influence of gaze direction on ERP components, most notably on the N170 amplitude, is far from being consistent or uniform. The effect is most likely modulated by several factors, such as face orientation and task demands or structures, and could be facilitated by dynamic or live presentation of stimuli. This review calls for further studies to systematically manipulate these factors to analyse their effects independently and also their potential interactions, which would help establish robust and standardised methods to evaluate gaze-related modulation of N170 component.

In addition, more systematic reporting of effect sizes, as well as improved accessibility to original datasets, will enable future evaluation of the robustness of the findings, with more quantitative approach such as meta-analyses. In fact, based on available data, we found evidence of possible small-study effects (publication bias), which could partly be due to the inconsistent reporting of effect sizes in previous studies. We provide the forest plots for the small number of studies which reported relevant information on effect sizes in [Supplementary Figs. 1–6](#), for references. We strongly recommend that a meta-analysis of the effects of perceived gaze on the N170 component be conducted in the future, when more studies start to systematically report the methodological details as well as power statistics (such as effect sizes), to assess the consistency and robustness of these results.

Our review also calls for researchers to report details of manipulations of stimuli and task and discuss the possible contribution of these factors on gaze-related ERPs, before generalising their findings across gaze processing in a wider context. Such systematic approaches would be fruitful to identify the neural mechanisms underlying gaze processing, and its impact on social interaction and communication, as well as the neurodevelopmental conditions affecting these domains. Understanding of gaze direction processing effects has a wide implication for social and cognitive neuroscience, in which gaze-related ERPs have a potential to be used as an endophenotype of clinical symptoms or diagnosis of atypical social development (e.g., [Elsabbagh et al., 2012](#)).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neubiorev.2022.104913](https://doi.org/10.1016/j.neubiorev.2022.104913).

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