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The influence of top-down modulation on the processing of direct gaze

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Running head: Direct Gaze Processing and Task-demand

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1 **Abstract**

2 Gaze or eye contact is one of the most important non-verbal social cues, which is
3 fundamental to human social interactions. To achieve real time and dynamic face-to-face
4 communication, our brain needs to process another person's gaze direction rapidly and
5 without explicit instruction. In order to explain fast and spontaneous processing of direct
6 gaze, the fast-track modulator model (Senju & Johnson, 2009) was proposed. Here, we
7 review recent developments in gaze processing research in the last decade to extend the
8 fast-track modulator model. In particular, we propose that task demand or top-down
9 modulation could play a more crucial role at gaze processing than formerly assumed. We
10 suggest that under different task demands, top-down modulation can facilitate or interfere
11 with the direct gaze effects for early visual processing. The proposed modification of the
12 model extends the role of task demand and its implication on the direct gaze effect, as well
13 as the need to better control for top-down processing in order to better disentangle the role
14 of top-down and bottom-up processing on the direct gaze effect.

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1 Introduction

2 Gaze processing plays a fundamental role in human social cognition. Eye contact is a
3 particularly important stimulus, working as threat signal for most primates (Emery, 2000),
4 but also as an affiliative signal in humans (Kleinke, 1986). As a powerful social stimulus, eye
5 contact communicates emotions and social intentions such as approach-oriented
6 motivations and general interests in the observer (Adams, Ambady, Macrae, & Kleck, 2006;
7 Adams & Kleck, 2005; George & Conty, 2008; Macrae, Hood, Milne, Rowe, & Mason, 2002).
8 Perception of direct gaze can affect social processing, having an effect on face processing in
9 various tasks. Direct gaze evokes positive social judgments (Bindemann, Mike Burton, &
10 Langton, 2008; Chen, Helminen, & Hietanen, 2017; Willis, Palermo, & Burke, 2011), increases
11 other's likability (Kuzmanovic et al., 2009; Mason, Tatkov, & Macrae, 2005), positively
12 affects attractiveness evaluations (Ewing, Rhodes, & Pellicano, 2010), biases face preference
13 (Jones, Debruine, Little, Conway, & Feinberg, 2006), triggers self-referential processes
14 (Conty, George, & Hietanen, 2016; Hietanen & Hietanen, 2017) and enhances interpersonal
15 synchronization (Patterson, 1982). Overall, direct gaze is acknowledged as highly important
16 in social perception, and its prioritized processing can be critical for social interaction
17 (Emery, 2000).

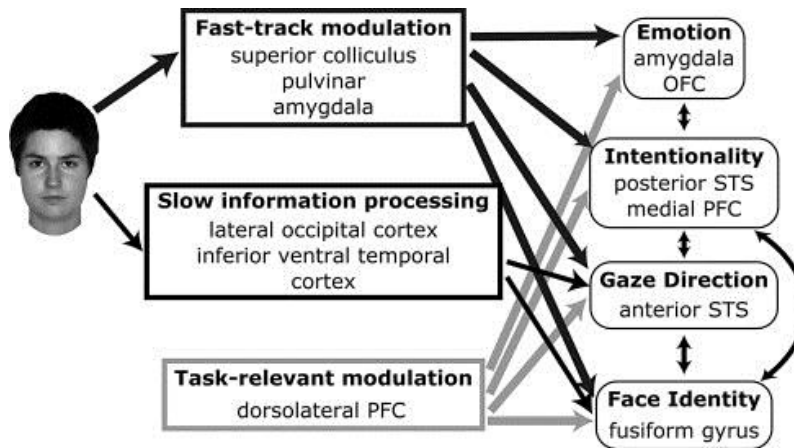
18 Direct gaze modulates other cognitive functions as well. For instance, direct gaze has
19 been shown to capture attention and be preferentially processed compared to averted gaze
20 in different tasks (e.g. Yokoyama et al., 2011; Palanica and Itier, 2012; Senju and Hasegawa,
21 2005). At a developmental level, human neonates and infants can discriminate between
22 averted and direct gaze, in adult faces (Farroni, Csibra, Simion, & Johnson, 2002; Hains &
23 Muir, 1996) and prefer direct-gaze faces (Farroni et al., 2002; Hains & Muir, 1996; Maurer,
24 1985). Direct gaze preference is also present in healthy adult human beings and behavioural

1 studies have shown that direct gaze can capture attention more readily compared to averted
2 gaze (Mares, Smith, Johnson, & Senju, 2016; Senju & Hasegawa, 2006), even when gaze is
3 task irrelevant (Conty, Tijus, Hugueville, Coelho, & George, 2006; Palanica & Itier, 2012;
4 Senju & Hasegawa, 2005; Vuilleumier, George, Lister, Armony, & Driver, 2005) or not
5 attended to (Yokoyama, Sakai, Noguchi, & Kita, 2014). Note that conversely, direct gaze
6 holds eye movements (Dalmaso, Castelli, & Galfano, 2017). Finally, face processing is
7 modulated by gaze direction in gender discrimination or identity recognition tasks (Burra,
8 Framorando, & Pegna, 2018; Hood, Macrae, Cole-Davies, & Dias, 2003; Macrae et al., 2002;
9 Vuilleumier et al., 2005). Taken together, several lines of research highlight the relevant role
10 of direct gaze as a social cue for human beings and its privileged processing in several tasks.

11 To account for the neural mechanisms underlying the preferential processing of
12 direct gaze, Senju and Johnson (2009) proposed the fast-track modulator model, which
13 extends a two-system theory, based on models of face processing divided into a subcortical
14 route (Conspec) and a cortical social brain network (Conlern) (Johnson & Morton, 1991;
15 Morton & Johnson, 1991). In the model of Senju and Johnson (2009), the authors proposed a
16 dual-route to process visual information, which allows for a 'fast-track' processing of direct
17 gaze, initially detected by a subcortical pathway (LeDoux, 1996), and a slow information-
18 processing pathway situated in cortical visual regions. This fast subcortical pathway has been
19 thought to modulate the cortical processing of social signals such as emotion, intentionality,
20 gaze direction and face identity.

21 In line with the hypothesised processing of direct gaze through the subcortical
22 pathway, several functional magnetic resonance imaging (fMRI) studies have reported the
23 contribution of subcortical structures in direct gaze perception. For instance, on rhesus
24 monkeys, a part of the amygdala, called the lateral extended amygdala (LEA, comprising the

1 central nucleus and the bed nucleus of the stria terminalis) was specifically sensitive to gaze
2 direction (Hoffman, Gothard, Schmid, & Logothetis, 2007). Similar findings have been
3 observed in humans, where greater right amygdala activation has been observed in response
4 to direct rather than averted gaze (Kawashima et al., 1999; Wicker, Perrett, Baron-Cohen, &
5 Decety, 2003). Accordingly, a recent study examined amygdala activation in healthy
6 participants and in a cortically blind patient, and the results showed greater activation in the
7 right amygdala in response to images of (neutral) faces with direct gaze as compared to
8 faces with averted gaze, both in healthy participants and in the cortically blind patient (Burra
9 et al., 2013). These findings suggest that amygdala responsivity does not even require an
10 intact primary visual cortex. Furthermore, other fMRI data revealed the relation between
11 subcortical and cortical regions, measuring an increased functional coupling between the
12 right fusiform gyrus, an area specialized in face processing, and the right amygdala for direct
13 compared to averted gaze (George, Driver, & Dolan, 2001). Finally, studies with patients
14 suffering from amygdala lesions have shown that they do not look at the eye region the
15 same way as controls do (Gamer, Schmitz, Tittgemeyer, & Schilbach, 2013; Spezio, Huang,
16 Castelli, & Adolphs, 2007), and that they do not show gaze-cued attention orienting
17 (Akiyama et al., 2006). In sum, these findings fit the fast-track modulator model, which
18 proposed the involvement of a subcortical pathway for direct eye gaze detection (but see:
19 Mormann et al., 2015). It is also consistent with a claim that direct gaze would be
20 preferentially processed in a rather involuntary manner (for a similar conclusion in other
21 studies using different experimental manipulations, see Madipakkam, Rothkirch,
22 Guggenmos, Heinz, & Sterzer, 2015; Stein, Senju, Peelen, & Sterzer, 2011; Yokoyama,
23 Noguchi, & Kita, 2013; Yokoyama et al., 2014).



1

2 **Figure 1.** Schematic depiction of the fast-track modulator model (Senju & Johnson, 2009).

3 Besides the involvement of subcortical regions, the fast-track modulator model also
 4 proposed that the detection of direct gaze is 'fast', and, therefore, would occur at a very
 5 early stage in the visual processing. It is therefore crucial to evaluate the timing of direct
 6 gaze processing. Electrophysiology, especially through the use of electroencephalography
 7 (EEG) or magnetoencephalography (MEG), provides evidence of cognitive processing with
 8 high temporal resolution (at the millisecond scale), and is informative for early neural coding
 9 of direct gaze. However, one clear limitation should be noted. These techniques that usually
 10 record neural activity at the scalp level, do not easily allow for the direct measurement of
 11 the subcortical structures critical for the fast-track modulation model. Consequently, they
 12 typically measure cortical activity of brain regions, which are hypothesised to be modulated
 13 by subcortical activation (but see Mares, Smith, Johnson & Senju, 2018, for an effect of
 14 direct gaze on the N170 component independent of the subcortical pathway). Such brain
 15 regions, defined as a so-called 'social brain network' (Brothers, 1990; Grossmann & Johnson,
 16 2007), include the fusiform gyrus, the anterior and posterior parts of the superior temporal
 17 sulcus (STS), and the medial pre-frontal and orbitofrontal cortex - regions that have been
 18 proposed to be modulated by the subcortical pathway via the amygdala. Typically, gaze

1 perception research has been focused on the electric N170 (or the magnetic M170), an early
2 face-sensitive component, occurring over occipitotemporal sites between 130 and 200 ms
3 after face presentation (Bentin, Allison, Puce, Perez, & McCarthy, 1996). This component is
4 sensitive to the face configuration and it is thought to reflect the initial process of integrating
5 facial features into a holistic percept (Eimer, 2000; Sagiv & Bentin, 2001). Conty, N'Diaye,
6 Tijus, and George (2007) found that the effect of eye contact appeared in this component,
7 occurring as early as 150–170 ms after stimulus onset.

8 However, studies have reported highly inconsistent neural activity for direct,
9 compared to averted, gaze direction. Some research has reported a larger amplitude of
10 N170 to averted gaze, compared to eye contact in static gaze, while other studies have
11 measured the opposite effect or no effect at all (Grice et al., 2005; Klucharev & Sams, 2004;
12 Schweinberger, Kloth, & Jenkins, 2007; Taylor, Itier, Allison, & Edmonds, 2001). Some argued
13 that discrepancies between studies could be due to the differences in the tasks used (for
14 instance: Itier & Batty, 2009; Nummenmaa & Calder, 2009). For example, some EEG studies
15 have used passive viewing tasks (Caruana et al., 2014; Puce, Smith, & Allison, 2000;
16 Watanabe, Miki, & Kakigi, 2002). By contrast, other studies used explicit tasks, in which
17 participants were required to report whether the gaze was oriented away or toward them
18 (Conty et al., 2007; Itier, Alain, Kovacevic, & McIntosh, 2007). Overall, the results of the N170
19 behaviour on gaze direction remains inconsistent.

20 To date, the impact of task-relevant demand provided by task structure and context
21 on gaze direction processing has not generally been fully explored (but see Itier, Alain,
22 Sedore, & McIntosh, 2007). However, accumulating evidence started to suggest that
23 diversity in the context and task-demand can be a potential source of inconsistency in the
24 previous literature. For example, task demand and social context can be associated to top

1 down modulation via the prefrontal cortex, of key cortical structures, such as the fusiform
2 gyrus (Itier and Taylor, 2002, Rossion et al., 2003, Watanabe et al., 2003) or the STS (Batty
3 and Taylor, 2003, Henson et al., 2003, Itier et al., 2006, Itier and Taylor, 2004, Watanabe et
4 al., 2003), that constitute the main sources of the N170 (for instance, Deffke et al., 2007;
5 Itier & Taylor, 2004; Plomp, Michel, & Herzog, 2010). Therefore, top-down processing might
6 prioritize or inhibit the processing of specific facial information depending on the task
7 demands and context. This might result in discrepancies for direct gaze processing at a
8 behavioural level (see opposite results of: see opposite results of: Macrae et al., 2002;
9 Vuilleumier et al., 2005) or at an electrophysiological level, as it has been already detailed.

10 One such example has been provided by Latinus et al. (2015). The authors used two
11 different tasks with the same stimulus presentation as Conty et al. (2006). Specifically, they
12 manipulated the task demand by using a 'social' task (discriminating gaze towards vs. away
13 from me) and a non-social task (discriminating gaze to the left vs. right). When participants
14 made a non-social judgment, the N170 component was significantly larger to any gaze shift
15 away from, than towards, the observer. This occurred for stimuli depicting both direct gaze
16 and intermediately averted gaze. However, when subjects made social judgments, the effect
17 was attenuated in the right hemisphere, where the N170 amplitudes were not consistently
18 larger for gaze shifts away from the observer. In sum, they claimed that the handling of
19 these 'modes' in some experiments and not in others might explain the discrepancies in the
20 prior literature. Thus, this activation of the social brain network mode would influence which
21 regions are activated during eye contact. The dissociation between the 'social' and 'non-
22 social' modes of information processing of gaze in the brain might help to reconcile the
23 different results observed in the literature.

1 However, an alternative possibility is that social and non-social tasks can be
2 associated with different demands and thus engage a different set of cognitive processing.
3 Specifically, in a dynamic presentation of gaze shifts, a left/right discrimination of eye
4 movement requires only a local motion detection without detailed gaze processing, while
5 distinguishing between towards/away would require a more global conceptual processing,
6 including a representation of gaze direction with respect to the observer point of view. Thus,
7 it is possible that different task demands associated with the processing of different 'modes',
8 rather than the processing of different 'modes' per se, could account for the effect of direct
9 gaze on cognitive (attentional capture) and neural processing (ERPs) reported in previous
10 studies.

11 This critical importance of task demand on cognitive processing in general has been
12 well documented throughout the last decades. In visual cognition research for instance, the
13 role of top-down processing (task at hand) on bottom-up attention (stimulus on screen) has
14 been prominently investigated (Folk & Remington, 1998; Theeuwes, 1992). Some have
15 demonstrated that despite being totally irrelevant, highly salient distractors capture
16 attention (Theeuwes, 1992). In other words, low-level saliency, which is computed in an
17 early stage of visual processing, can alter later attention selection. However, different
18 studies have revealed that task-set or task demand (i.e. taking into account relevant
19 information and/or suppressing irrelevant information) can reduce or even abolish the
20 capture effect. In their seminal study, Folk & Remington (1998) revealed that a task-
21 irrelevant but salient distractor (i.e. a red stimulus) captured attention only when a matching
22 feature defined the relevant target, i.e. colour in this example. When the relevant target was
23 defined by another feature (for instance its shape or size), the attentional capture effect
24 vanished.

1 Nonetheless, despite the well-known effects of task demand in visual attention, in
2 the context of social cognition and more specifically, gaze processing, there is still limited
3 understanding about the role of task demand.

4 In the following section of this article, we highlight the possible role of task-relevant
5 or top-down modulations on gaze processing and its related neural mechanisms. In general,
6 top-down modulation increases the sensitivity of our perceptual system to task-relevant
7 information - prioritization - with respect to the ongoing task (Kastner & Ungerleider, 2000).
8 Such prioritization will increase the gain or sensitivity of the cortical pathway, in order to
9 perform the task with minimum demand (for instance, see Herrmann, Montaser-Kouhsari,
10 Carrasco, & Heeger, 2010). In the context of gaze perception, this modulation would enable
11 our perceptual system to preferentially prioritize direct gaze over averted gaze or closed
12 eyes when it is task/context appropriate, and critically, it can also be gated or attenuated at
13 an early stage if the eyes or faces are task or self-irrelevant or even if averted gaze is more
14 relevant for the current task. In other words, top-down modulation can have an effect on
15 the perception of direct gaze at an early stage of visual processing.

16 Here, we summarise two lines of evidence that task demands can influence the
17 processing of direct gaze, one at a behavioural level and the other at an electrophysiological
18 level.

19 In the first line of evidence, a recent study of ours (Framorando, George, Kerzel, &
20 Burra, 2017) revealed the influence of task demand on the “stare-in-the-crowd’ effect (von
21 Grünau & Anston, 1995), which is defined as a faster and more efficient detection of direct
22 gaze over averted gaze in a visual search task. In a series of behavioural experiments,
23 Framorando et al. (2017) demonstrated that the faster processing of faces with direct gaze
24 over averted gaze was only present when attention was focused on the target face *and*

1 when task demand required the processing of the facial features including eyes. They used
2 one target face, with eyes straight or averted, surrounded by faces with closed eyes, similar
3 to Experiment 3 of Cooper, Law, & Langton (2013), and did not observe a “stare-in-the-
4 crowd” effect in this condition, replicating Cooper et al. (2013) and suggesting that, in
5 addition to top-down modulation, low-level of visual perception (e.g. presence/absence of
6 white sclera or relationship between target and distractors) can dramatically influence the
7 “stare-in-the-crowd” effect. However, using the same stimuli, they could observe the “stare-
8 in-the-crowd” effect when they changed the task so that participants were required to
9 process the eye region in a gaze direction or gender task, as gender discrimination also
10 involves encoding information from eye region (Brown & Perrett, 1993; Dupuis-Roy, Fortin,
11 Fiset, & Gosselin, 2009; Schyns, Bonnar, & Gosselin, 2002; Yamaguchi, Hirukawa, &
12 Kanazawa, 1995; Zhao & Hayward, 2010), The results suggest that a task where encoding of
13 the eyes is needed can facilitate the "stare-in-the-crowd" effect even in stimuli for which this
14 effect would otherwise not be present.

15 In addition, in the same study, Framorando et al. demonstrated that direct gaze failed
16 to capture observers’ attention when gaze direction was completely irrelevant and
17 competed for selection with another face relevant target. Using the same visual arrays as
18 their other experiments reported above, they applied the “additional singleton paradigm”
19 (Theeuwes, 1992), in which participants were required to focus their attention to a target
20 face with closed eyes defined by its orientation (tilted to the left or right). Crucially, one of
21 the face distractors, either with straight gaze or an averted gaze, competed for selection
22 with the target, defined as neutral face with closed eyes tilted in a slightly different
23 orientation than others faces. As a result, the presence of a distractor slowed target
24 detection, which was unaffected by the gaze direction of the distractor. This result may also

1 seem inconsistent with data revealing attentional capture by task-irrelevant direct gaze or
2 preferential detection of direct gaze under continuous flash suppression (CFS) presentation
3 (Rothkirch, Madipakkam, Rehn, & Sterzer, 2015; Stein et al., 2011). A possible reason for
4 such discrepancies might relate to the task used with some studies requiring the detection of
5 a change in eye direction (Yokoyama, Ishibashi, Hongoh, & Kita, 2011), a change between
6 face arrayss (Lyyra, Astikainen, & Hietanen, 2018) or the detection of a face target (Rothkirch
7 et al., 2015; Stein et al., 2011; for the implication on top-down modulation on CFS, see the
8 critical review of Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014). In the attentional
9 capture experiment of Framorando et al, study, by contrast, gaze was never relevant
10 because the target was discernible by a low-level feature (i.e. its orientation with respect to
11 other stimuli on screen). Moreover, the target competed for selection simultaneously with
12 another face distractor (Rothkirch et al., 2015; Stein et al., 2011), which is a prerequisite of
13 attentional capture effect (for more details, see the review of Theeuwes, 2010). In sum, by
14 reducing as much as possible the impact of top-down processing that might influence
15 attentional capture effect, this study failed to reveal an attentional capture by direct gaze
16 over averted gaze.

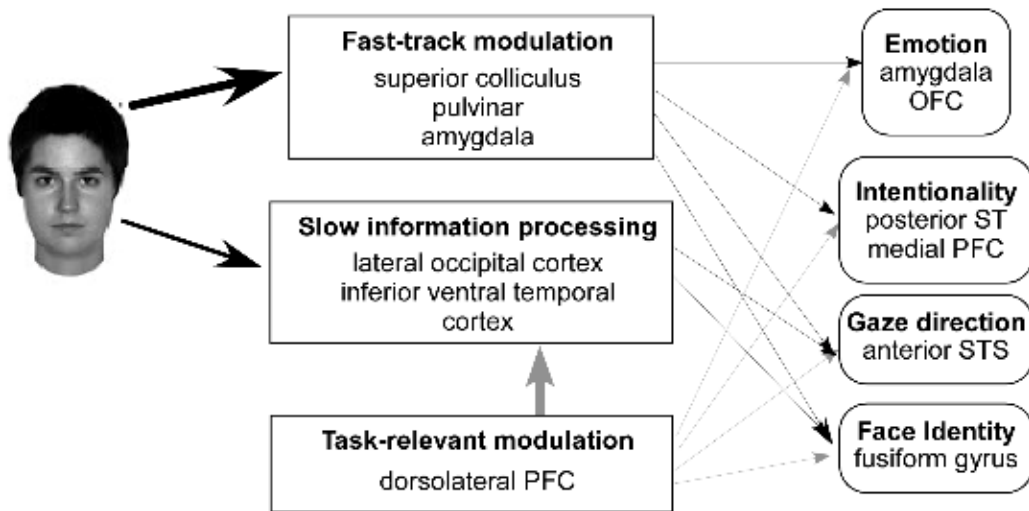
17 The second line of evidence (Burra et al., 2018) highlights the critical role of task
18 demand on early cortical processing of gaze processing, even earlier than previously
19 measured (Latinus et al., 2015). In this study, in Experiment 1, the authors used a gender
20 categorization task of faces (cropped to avoid the use external features to perform the task).
21 Despite a lack of an effect of gaze on the N170, the amplitude of P1 component, which peaks
22 at around 100 ms following stimulus onset in adults, was larger for faces with direct gaze
23 than those with averted gaze or closed eyes. Visual P1 (or P100) is thought to originate from
24 striate and extrastriate visual areas (e.g. Clark & Hillyard, 1996; Di Russo, Martinez, &

1 Hillyard, 2003), and is known to be sensitive to many low-level properties of visual stimuli
2 (see Regan, 1989). Previous studies in adults have reported a larger P1 (or M1 in MEG) in
3 response to faces than to objects (e.g. Eimer, 1998; Eimer & Holmes, 2002; Goffaux,
4 Gauthier, & Rossion, 2003; Itier & Taylor, 2004), suggesting the face sensitivity of this
5 component. The result reported in Burra et al. (2018) is consistent with different pieces of
6 evidence which already revealed modulations of P1 by gaze direction (Berchio et al., 2016;
7 Burra, Kerzel, & George, 2016; Doi, Sawada, & Masataka, 2007; Schyns, Petro, & Smith,
8 2007; Tye et al., 2013).

9 Critically, Burra et al. (2018) demonstrated that the P1 amplitude modulation is
10 dependent on the task demand. However, due to the P1 sensitivity to many low-level
11 properties of visual stimuli (see Regan, 1989), the authors could not rule out the
12 repercussion of such properties in their P1 effect. To address this point, in their second
13 experiment, they used the same stimuli, but with a different task in which participants were
14 instructed to detect the presence of a non-social stimulus (a house) among faces. In this
15 study, where gaze direction was irrelevant, the P1 amplitude was not modulated by gaze
16 direction. These results show that P1 modulation by direct gaze is task dependent.

17 In its initial version, the fast-track modulator model implied that early cortical
18 processing of direct gaze was immune to task-relevant modulation. Accordingly, the model
19 did not predict a modulation of gaze processing at the early stage of visual processing, such
20 as the P1 component, which is generated in multiple extra striate cortical areas, including
21 the mid-occipital gyri (Di Russo et al., 2003; Foxe & Simpson, 2002), corresponding to the
22 slow information-processing module. Thus, to account for the observed top-down
23 modulation on direct gaze processing at an earlier stage of visual processing (Burra et al.,
24 2018) and other recent evidence highlighting the role of task demands and structures on

1 direct gaze processing (Framorando et al., 2017; Latinus et al., 2015), we propose that the
 2 modulation of slow information processing of gaze direction is mediated by task demand, as
 3 depicted in Figure 2.



4

5 **Figure 2.** Modification of the fast-track modulator model (Senju & Johnson, 2009). We
 6 included an arrow from the task-relevant modulation and slow information processing.

7

8 In this opinion paper, we highlighted the critical role of top-down processing in gaze
 9 perception, especially at an early stage of visual processing. The fast-track modulator model
 10 has been proposed to explain the underpinnings of such gaze processing. Despite the fact
 11 that key cerebral regions included in the model have been associated with gaze processing,
 12 their dynamic function still remains unclear, and the critical role of the task-relevant
 13 modulation is still poorly understood in this model. Here, we suggest that, by default,
 14 subcortical activation is modulated by the presence of direct gaze over averted gaze.
 15 However, at a cortical level, when the eye region, or gaze direction, is task-relevant, top-
 16 down processing might increase the sensitivity of our perceptual and attentional system to

1 the eyes (direct or averted with respect to the current task). By contrast, it could also reduce
2 the sensitivity to the eyes if the eye region is task-irrelevant (Burra et al., 2018; Latinus et al.,
3 2015) and prevent attentional capture by direct gaze (Framorando et al., 2017). Therefore,
4 task relevance might play a crucial role in the detection of direct gaze at early stage of visual
5 processing. This argument extends the ‘task-relevant modulation’ proposed in Senju and
6 Johnson (2009), and proposes that task demand can modulate the impact of direct gaze
7 from an early stage of visual processing.. Unfortunately, in many cases it is assumed that
8 cortical responses, especially those measured by ERP at an early stage of visual perception,
9 reflect the neural correlate of a stimulus that is automatically triggered by a fully bottom-up
10 process, which is fully dependent on the processing of immediately available stimulus,
11 without an influence of any voluntary strategy or contextual modulation. However, as
12 discussed in the previous sections, task demands can impact visual perception at an early
13 stage, especially when the task and stimuli remain stable among trials. In other words, the
14 constancy of the displayed stimuli could allow observers to use particular strategies that rely
15 on holistic or feature processing, altering task demands. Here we propose several possible
16 strategies to control top-down modulation to further examine the role of bottom-up
17 attention on gaze processing. Firstly, we would want to remove external features such as
18 accessory or hair, which could allow participants to devise an alternative strategy to perform
19 the task (e.g. gender categorization task) without relying on features around the eyes. If
20 possible it would be ideal that only the facial features are displayed, not the totality of the
21 face. Secondly, we could adopt a random display of stimuli at different locations on the
22 screen (left, right, upper or lower location from the fixation cross) if appropriate, because a
23 constant position of the stimulus on the screen could increase the likelihood of using a
24 specific strategy to perform the task, such as using specific facial features (for instance, the

1 use of the size of the eyebrows or the mouth in gender categorization tasks). Thirdly, we
2 could change the task at every trial by using a cue or by asking participants to perform the
3 task with respect to a specific dimension following each trial (for instance, Gender:
4 male/female; Gaze direction: direct/averted; Age: old-young; Head direction: frontal-
5 deviated), since the use of the same task during the experiment might give rise to specific
6 strategies, which could prompt a specific top-down control and mask bottom-up processes.
7 This design would make it more difficult for participants to adopt a strategy to give larger
8 weight to the task-relevant information or discount task-irrelevant information, which could
9 reduce bottom-up processing (Belopolsky, Schreij, & Theeuwes, 2010; Burra & Kerzel, 2013;
10 Folk & Remington, 1992). Finally, we could measure inter-individual differences
11 systematically, to rule out effects associated with personality traits. Measures of personality
12 traits, such as anxiety, social anxiety, autism, extraversion or even attachment, are known to
13 influence gaze perception (Burra, Massait, & Vrticka, 2019; Cecchini, Iannoni, Pandolfo,
14 Aceto, & Lai, 2015; Nummenmaa, Engell, von dem Hagen, Henson, & Calder, 2012; Ponari,
15 Trojano, Grossi, & Conson, 2013; Robson, 1967; Schulze, Renneberg, & Lobmaier, 2013). It is
16 possible that these personality traits could drive some participants to employ specific
17 strategies to perform different tasks, which might affect their behavioural and cerebral
18 response.

19 It is also crucial to evaluate the role of the top-down processes on gaze processing in
20 clinical populations. In fact, deficits in eye and gaze processing are a major impairment in
21 autism (American Psychiatric Association, 2013; Forgeot d'Arc et al., 2017; Leekam,
22 Hunnisett, & Moore, 1998), and have been reported in different pathologies such as
23 prosopagnosia (Caldara et al., 2005; Campbell, Heywood, Cowey, Regard, & Landis, 1990;
24 but see Duchaine, Jenkins, Germine, & Calder, 2009; Pancaroglu et al., 2016) or even

1 schizophrenia (Hooker & Park, 2005). However, to our knowledge, few studies have
2 investigated the role of the task demand on gaze processing in these clinical populations.
3 Specifically, a lack of typical gaze processing in these clinical populations could be due to a
4 functional impairment that reduces gaze processing when it is not mandatory for the task,
5 rather than an impairment in the neural mechanisms underlying gaze perception per se. For
6 instance, in a prior study, we demonstrated that PS, a patient suffering from acquired
7 prosopagnosia, was insensitive to implicit attentional deployment to gaze direction, despite
8 being able to explicitly discriminate gaze direction (Burra, Kerzel, & Ramon, 2017). Such
9 dissociation between explicit and implicit performance is of major interest in understanding
10 the underpinnings of prosopagnosia or other populations suffering from a deficit in social
11 cognition and should be more frequently evaluated in order to ascertain the extent to which
12 the deficit is stimulus-driven or mediated by task demand.

13 Finally, the fast-track modulator model might be subject to further modifications.
14 Some additional updates might be included in the future. For instance, despite the likelihood
15 (Jiang, Borowiak, Tudge, Otto, & von Kriegstein, 2017) that slow cortical information
16 processing (at P1 level) and sub-cortical pathways communicate (Muller-Bardorff et al.,
17 2018; Rotshtein et al., 2010), to date, no clear evidence has revealed this connectivity, in the
18 context of gaze (for connectivity between amygdala and fusiform gyri in the context of gaze:
19 see George et al., 2001). Further studies, measuring fMRI connectivity (see the recent work
20 of Jiang et al., 2017) combined with EEG or even intracranial EEG study (in the amygdala) in
21 combination with electrocorticography (on the occipital cortex) could address this question.
22 These combined methodologies would also help us understand the extent to which task
23 demand might functionally impact such functional connectivity.

1 In conclusion, we believe that investigating the role of the top-down process in the
2 fast-track modulator model and its influence at an early stage of face processing will
3 increase the reliability of the model. Moreover, the understanding of the balance between
4 task demand and stimulus-driven mechanisms in gaze perception will increase the possibility
5 of prediction based on different a priori aspects (task demand, inter-individual differences,
6 and stimuli) that enable a better understanding of gaze processing in both the typical and
7 clinical populations.

8

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12 schmidheiny.ch/informations.html).

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1 **References**

- 2 Adams, R. B., Ambady, N., Macrae, C. N., & Kleck, R. E. (2006). Emotional expressions
3 forecast approach-avoidance behavior. *Motivation and Emotion, 30*(2), 179-188.
4 doi:10.1007/s11031-006-9020-2
- 5 Adams, R. B., & Kleck, R. E. (2005). Effects of direct and averted gaze on the perception of
6 facially communicated emotion. *Emotion, 5*(1), 3-11. doi:10.1037/1528-3542.5.1.3
- 7 Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Umeda, S., & Kashima, H. (2006). Gaze but
8 not arrows: a dissociative impairment after right superior temporal gyrus damage.
9 *Neuropsychologia, 44*(10), 1804-1810.
- 10 American Psychiatric Association. (2013). Autism Spectrum Disorder. In *Diagnostic and*
11 *statistical manual of mental disorders; DSM-V* (5th ed.). Washington, DC.
- 12 Belopolsky, A. V., Schreij, D., & Theeuwes, J. (2010). What is top-down about contingent
13 capture? *Attention, Perception, & Psychophysics, 72*(2), 326-341.
- 14 Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological Studies
15 of Face Perception in Humans. *J Cogn Neurosci, 8*(6), 551-565.
16 doi:10.1162/jocn.1996.8.6.551
- 17 Berchio, C., Rihs, T. A., Piguet, C., Dayer, A. G., Aubry, J. M., & Michel, C. M. (2016). Early
18 averted gaze processing in the right Fusiform Gyrus: An EEG source imaging study.
19 *Biol Psychol, 119*, 156-170. doi:10.1016/j.biopsycho.2016.06.008
- 20 Bindemann, M., Mike Burton, A., & Langton, S. R. (2008). How do eye gaze and facial
21 expression interact? *Visual Cognition, 16*(6), 708-733.
- 22 Brothers, L. (1990). The Neural Basis of Primate Social Communication. *Motivation and*
23 *Emotion, 14*(2), 81-91. doi:Doi 10.1007/Bf00991637

- 1 Brown, E., & Perrett, D. I. (1993). What gives a face its gender? *Perception*, 22(7), 829-840.
2 doi:10.1068/p220829
- 3 Burra, N., Framorando, D., & Pegna, A. J. (2018). Early and late cortical responses to directly
4 gazing faces are task dependent. *Cogn Affect Behav Neurosci*. doi:10.3758/s13415-
5 018-0605-5
- 6 Burra, N., Hervais-Adelman, A., Kerzel, D., Tamietto, M., de Gelder, B., & Pegna, A. J. (2013).
7 Amygdala activation for eye contact despite complete cortical blindness. *J Neurosci*,
8 33(25), 10483-10489. doi:10.1523/JNEUROSCI.3994-12.2013
- 9 Burra, N., & Kerzel, D. (2013). Attentional capture during visual search is attenuated by
10 target predictability: evidence from the N2pc, Pd, and topographic segmentation.
11 *Psychophysiology*, 50(5), 422-430. doi:10.1111/psyp.12019
- 12 Burra, N., Kerzel, D., & George, N. (2016). Early Left Parietal Activity Elicited by Direct Gaze: A
13 High-Density EEG Study. *PLoS One*, 11(11), e0166430.
14 doi:10.1371/journal.pone.0166430
- 15 Burra, N., Kerzel, D., & Ramon, M. (2017). Gaze-cueing requires intact face processing -
16 Insights from acquired prosopagnosia. *Brain Cogn*, 113, 125-132.
17 doi:10.1016/j.bandc.2017.01.008
- 18 Burra, N., Massait, S., & Vrticka, P. (2019). Differential impact of trait, social, and attachment
19 anxiety on the stare-in-the-crowd effect. *Scientific reports*.
- 20 Caldara, R., Schyns, P., Mayer, E., Smith, M. L., Gosselin, F., & Rossion, B. (2005). Does
21 prosopagnosia take the eyes out of face representations? Evidence for a defect in
22 representing diagnostic facial information following brain damage. *J Cogn Neurosci*,
23 17(10), 1652-1666. doi:10.1162/089892905774597254

- 1 Campbell, R., Heywood, C. A., Cowey, A., Regard, M., & Landis, T. (1990). Sensitivity to eye
2 gaze in prosopagnosic patients and monkeys with superior temporal sulcus ablation.
3 *Neuropsychologia*, *28*(11), 1123-1142. doi:Doi 10.1016/0028-3932(90)90050-X
- 4 Caruana, F., Cantalupo, G., Lo Russo, G., Mai, R., Sartori, I., & Avanzini, P. (2014). Human
5 cortical activity evoked by gaze shift observation: an intracranial EEG study. *Hum*
6 *Brain Mapp*, *35*(4), 1515-1528. doi:10.1002/hbm.22270
- 7 Cecchini, M., Iannoni, M. E., Pandolfo, A. L., Aceto, P., & Lai, C. (2015). Attachment style
8 dimensions are associated with brain activity in response to gaze interaction. *Soc*
9 *Neurosci*, *10*(3), 282-293. doi:10.1080/17470919.2014.998344
- 10 Chen, T., Helminen, T. M., & Hietanen, J. K. (2017). Affect in the eyes: explicit and implicit
11 evaluations. *Cogn Emot*, *31*(6), 1070-1082. doi:10.1080/02699931.2016.1188059
- 12 Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention affects early extrastriate but
13 not striate components of the visual evoked potential. *J Cogn Neurosci*, *8*(5), 387-
14 402. doi:10.1162/jocn.1996.8.5.387
- 15 Conty, L., George, N., & Hietanen, J. K. (2016). Watching Eyes effects: When others meet the
16 self. *Conscious Cogn*, *45*, 184-197. doi:10.1016/j.concog.2016.08.016
- 17 Conty, L., N'Diaye, K., Tijus, C., & George, N. (2007). When eye creates the contact! ERP
18 evidence for early dissociation between direct and averted gaze motion processing.
19 *Neuropsychologia*, *45*(13), 3024-3037. doi:10.1016/j.neuropsychologia.2007.05.017
- 20 Conty, L., Tijus, C., Hugueville, L., Coelho, E., & George, N. (2006). Searching for asymmetries
21 in the detection of gaze contact versus averted gaze under different head views: a
22 behavioural study. *Spat Vis*, *19*(6), 529-545.

- 1 Cooper, R. M., Law, A. S., & Langton, S. R. (2013). Looking back at the stare-in-the-crowd
2 effect: Staring eyes do not capture attention in visual search. *Journal of Vision*, 13(6),
3 10.
- 4 Dalmaso, M., Castelli, L., & Galfano, G. (2017). Attention holding elicited by direct-gaze faces
5 is reflected in saccadic peak velocity. *Experimental Brain Research*, 235(11), 3319-
6 3332. doi:10.1007/s00221-017-5059-4
- 7 Deffke, I., Sander, T., Heidenreich, J., Sommer, W., Curio, G., Trahms, L., & Lueschow, A.
8 (2007). MEG/EEG sources of the 170-ms response to faces are co-localized in the
9 fusiform gyrus. *NeuroImage*, 35(4), 1495-1501.
10 doi:10.1016/j.neuroimage.2007.01.034
- 11 Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical
12 activity during visuo-spatial attention. *Cerebral Cortex*, 13(5), 486-499.
- 13 Doi, H., Sawada, R., & Masataka, N. J. B. R. (2007). The effects of eye and face inversion on
14 the early stages of gaze direction perception—An ERP study. *1183*, 83-90.
- 15 Duchaine, B., Jenkins, R., Germine, L., & Calder, A. J. (2009). Normal gaze discrimination and
16 adaptation in seven prosopagnosics. *Neuropsychologia*, 47(10), 2029-2036.
17 doi:10.1016/j.neuropsychologia.2009.03.011
- 18 Dupuis-Roy, N., Fortin, I., Fiset, D., & Gosselin, F. (2009). Uncovering gender discrimination
19 cues in a realistic setting. *J Vis*, 9(2), 10 11-18. doi:10.1167/9.2.10
- 20 Eimer, M. (1998). Does the face-specific N170 component reflect the activity of a specialized
21 eye processor? *NeuroReport*, 9(13), 2945-2948.
- 22 Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural
23 encoding of faces. *NeuroReport*, 11(10), 2319-2324.

- 1 Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face
2 processing. *NeuroReport*, *13*(4), 427-431.
- 3 Emery, N. J. (2000). The eyes have it: the neuroethology, function and evolution of social
4 gaze. *Neurosci Biobehav Rev*, *24*(6), 581-604.
- 5 Ewing, L., Rhodes, G., & Pellicano, E. (2010). Have you got the look? Gaze direction affects
6 judgements of facial attractiveness. *Visual Cognition*, *18*(3), 321-330.
- 7 Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans
8 from birth. *Proc Natl Acad Sci U S A*, *99*(14), 9602-9605. doi:10.1073/pnas.152159999
- 9 Folk, C. L., & Remington, R. (1998). Selectivity in distraction by irrelevant featural singletons:
10 evidence for two forms of attentional capture. *J Exp Psychol Hum Percept Perform*,
11 *24*(3), 847-858. doi:Doi 10.1037/0096-1523.24.3.847
- 12 Folk, C. L., & Remington, R. W. (1992). Apparent Motion, Attentional Capture, and Inhibitory
13 Attentional Control Settings. *Bulletin of the Psychonomic Society*, *30*(6), 481-481.
- 14 Forgeot d'Arc, B., Delorme, R., Zalla, T., Lefebvre, A., Amsellem, F., Moukawane, S., . . .
15 Ramus, F. (2017). Gaze direction detection in autism spectrum disorder. *Autism*,
16 *21*(1), 100-107. doi:10.1177/1362361316630880
- 17 Foxe, J. J., & Simpson, G. V. (2002). Flow of activation from V1 to frontal cortex in humans. A
18 framework for defining "early" visual processing. *Experimental Brain Research*,
19 *142*(1), 139-150. doi:10.1007/s00221-001-0906-7
- 20 Framorando, D., George, N., Kerzel, D., & Burra, N. (2017). Straight gaze facilitates face
21 processing but does not cause involuntary attentional capture. *Visual Cognition*, 1-11.
- 22 Gamer, M., Schmitz, A. K., Tittgemeyer, M., & Schilbach, L. (2013). The human amygdala
23 drives reflexive orienting towards facial features. *Curr Biol*, *23*(20), R917-918.
24 doi:10.1016/j.cub.2013.09.008

- 1 George, N., & Conty, L. (2008). Facing the gaze of others. *Neurophysiol Clin*, *38*(3), 197-207.
2 doi:10.1016/j.neucli.2008.03.001
- 3 George, N., Driver, J., & Dolan, R. J. (2001). Seen gaze-direction modulates fusiform activity
4 and its coupling with other brain areas during face processing. *NeuroImage*, *13*(6 Pt
5 1), 1102-1112. doi:10.1006/nimg.2001.0769
- 6 Goffaux, V., Gauthier, I., & Rossion, B. (2003). Spatial scale contribution to early visual
7 differences between face and object processing. *Brain Res Cogn Brain Res*, *16*(3),
8 416-424.
- 9 Grice, S. J., Halit, H., Farroni, T., Baron-Cohen, S., Bolton, P., & Johnson, M. H. (2005). Neural
10 correlates of eye-gaze detection in young children with autism. *Cortex*, *41*(3), 342-
11 353.
- 12 Grossmann, T., & Johnson, M. H. (2007). The development of the social brain in human
13 infancy. *Eur J Neurosci*, *25*(4), 909-919. doi:10.1111/j.1460-9568.2007.05379.x
- 14 Hains, S. M., & Muir, D. W. (1996). Infant sensitivity to adult eye direction. *Child Dev*, *67*(5),
15 1940-1951.
- 16 Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., & Heeger, D. J. (2010). When size
17 matters: attention affects performance by contrast or response gain. *Nat Neurosci*,
18 *13*(12), 1554-1559. doi:10.1038/nn.2669
- 19 Hietanen, J. O., & Hietanen, J. K. (2017). Genuine eye contact elicits self-referential
20 processing. *Conscious Cogn*, *51*, 100-115. doi:10.1016/j.concog.2017.01.019
- 21 Hoffman, K. L., Gothard, K. M., Schmid, M. C., & Logothetis, N. K. (2007). Facial-expression
22 and gaze-selective responses in the monkey amygdala. *Curr Biol*, *17*(9), 766-772.
23 doi:10.1016/j.cub.2007.03.040

- 1 Hood, B. M., Macrae, C. N., Cole-Davies, V., & Dias, M. (2003). Eye remember you: the
2 effects of gaze direction on face recognition in children and adults. *Developmental*
3 *Science*, 6(1), 67-71. doi:Doi 10.1111/1467-7687.00256
- 4 Hooker, C., & Park, S. (2005). You must be looking at me: the nature of gaze perception in
5 schizophrenia patients. *Cogn Neuropsychiatry*, 10(5), 327-345.
6 doi:10.1080/13546800444000083
- 7 Itier, R. J., Alain, C., Kovacevic, N., & McIntosh, A. R. (2007). Explicit versus implicit gaze
8 processing assessed by ERPs. *Brain Res*, 1177, 79-89.
9 doi:10.1016/j.brainres.2007.07.094
- 10 Itier, R. J., Alain, C., Sedore, K., & McIntosh, A. R. (2007). Early face processing specificity: it's
11 in the eyes! *J Cogn Neurosci*, 19(11), 1815-1826. doi:10.1162/jocn.2007.19.11.1815
- 12 Itier, R. J., & Batty, M. (2009). Neural bases of eye and gaze processing: the core of social
13 cognition. *Neuroscience and Biobehavioral Reviews*, 33(6), 843-863.
14 doi:10.1016/j.neubiorev.2009.02.004
- 15 Itier, R. J., & Taylor, M. (2004). N170 or N1? Spatiotemporal differences between object and
16 face processing using ERPs. *Cerebral Cortex*, 14(2), 132-142.
- 17 Jiang, J., Borowiak, K., Tudge, L., Otto, C., & von Kriegstein, K. (2017). Neural mechanisms of
18 eye contact when listening to another person talking. *Soc Cogn Affect Neurosci*,
19 12(2), 319-328. doi:10.1093/scan/nsw127
- 20 Johnson, M., & Morton, J. (1991). Biology and cognitive development: The case of face
21 recognitionBlackwell. *New York*.
- 22 Jones, B. C., DeBruine, L. M., Little, A. C., Conway, C. A., & Feinberg, D. R. (2006). Integrating
23 gaze direction and expression in preferences for attractive faces. *Psychol Sci*, 17(7),
24 588-591. doi:10.1111/j.1467-9280.2006.01749.x

- 1 Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex.
2 *Annu Rev Neurosci*, 23, 315-341. doi:10.1146/annurev.neuro.23.1.315
- 3 Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., . . . Nakamura, K.
4 (1999). The human amygdala plays an important role in gaze monitoring. A PET
5 study. *Brain*, 122 (Pt 4), 779-783.
- 6 Kleinke, C. L. (1986). Gaze and eye contact: a research review. *Psychol Bull*, 100(1), 78-100.
- 7 Klucharev, V., & Sams, M. (2004). Interaction of gaze direction and facial expressions
8 processing: ERP study. *NeuroReport*, 15(4), 621-625.
- 9 Kuzmanovic, B., Georgescu, A. L., Eickhoff, S. B., Shah, N. J., Bente, G., Fink, G. R., & Vogeley,
10 K. (2009). Duration matters: dissociating neural correlates of detection and
11 evaluation of social gaze. *NeuroImage*, 46(4), 1154-1163.
12 doi:10.1016/j.neuroimage.2009.03.037
- 13 Latinus, M., Love, S. A., Rossi, A., Parada, F. J., Huang, L., Conty, L., . . . Puce, A. (2015). Social
14 decisions affect neural activity to perceived dynamic gaze. *Soc Cogn Affect Neurosci*,
15 10(11), 1557-1567. doi:10.1093/scan/nsv049
- 16 LeDoux, J. (1996). Emotional networks and motor control: a fearful view. *Progress in Brain*
17 *Research*, 107, 437-446.
- 18 Leekam, S. R., Hunnisett, E., & Moore, C. (1998). Targets and cues: gaze-following in children
19 with autism. *J Child Psychol Psychiatry*, 39(7), 951-962.
- 20 Lyyra, P., Astikainen, P., & Hietanen, J. K. (2018). Look at them and they will notice you:
21 Distractor-independent attentional capture by direct gaze in change blindness. *Visual*
22 *Cognition*, 26(1), 25-36. doi:10.1080/13506285.2017.1370052
- 23 Macrae, C. N., Hood, B. M., Milne, A. B., Rowe, A. C., & Mason, M. F. (2002). Are you looking
24 at me? Eye gaze and person perception. *Psychological Science*, 13(5), 460-464.

- 1 Madipakkam, A. R., Rothkirch, M., Guggenmos, M., Heinz, A., & Sterzer, P. (2015). Gaze
2 Direction Modulates the Relation between Neural Responses to Faces and Visual
3 Awareness. *J Neurosci*, *35*(39), 13287-13299. doi:10.1523/JNEUROSCI.0815-15.2015
- 4 Mares, I., Smith, M. L., Johnson, M. H., & Senju, A. (2016). Direct gaze facilitates rapid
5 orienting to faces: Evidence from express saccades and saccadic potentials. *Biol*
6 *Psychol*, *121*(Pt A), 84-90. doi:10.1016/j.biopsycho.2016.10.003
- 7 Mason, M. F., Tatkov, E. P., & Macrae, C. N. (2005). The look of love: gaze shifts and person
8 perception. *Psychol Sci*, *16*(3), 236-239. doi:10.1111/j.0956-7976.2005.00809.x
- 9 Maurer, D. (1985). Infants' perception of facedness. *Social perception in infants*.
- 10 Mormann, F., Niediek, J., Tudusciuc, O., Quesada, C. M., Coenen, V. A., Elger, C. E., &
11 Adolphs, R. (2015). Neurons in the human amygdala encode face identity, but not
12 gaze direction. *Nat Neurosci*, *18*(11), 1568-1570. doi:10.1038/nn.4139
- 13 Morton, J., & Johnson, M. H. (1991). CONSPEC and CONLERN: a two-process theory of infant
14 face recognition. *Psychol Rev*, *98*(2), 164-181.
- 15 Muller-Bardorff, M., Bruchmann, M., Mothes-Lasch, M., Zwitserlood, P., Schlossmacher, I.,
16 Hofmann, D., . . . Straube, T. (2018). Early brain responses to affective faces: A
17 simultaneous EEG-fMRI study. *NeuroImage*, *178*, 660-667.
18 doi:10.1016/j.neuroimage.2018.05.081
- 19 Nummenmaa, L., & Calder, A. J. (2009). Neural mechanisms of social attention. *Trends Cogn*
20 *Sci*, *13*(3), 135-143. doi:10.1016/j.tics.2008.12.006
- 21 Nummenmaa, L., Engell, A. D., von dem Hagen, E., Henson, R. N., & Calder, A. J. (2012).
22 Autism spectrum traits predict the neural response to eye gaze in typical individuals.
23 *NeuroImage*, *59*(4), 3356-3363. doi:10.1016/j.neuroimage.2011.10.075

- 1 Palanica, A., & Itier, R. J. (2012). Attention Capture by Direct Gaze is Robust to Context and
2 Task Demands. *J Nonverbal Behav*, *36*(2), 123-134. doi:10.1007/s10919-011-0128-z
- 3 Pancaroglu, R., Hills, C. S., Sekunova, A., Viswanathan, J., Duchaine, B., & Barton, J. J. (2016).
4 Seeing the eyes in acquired prosopagnosia. *Cortex*, *81*, 251-265.
5 doi:10.1016/j.cortex.2016.04.024
- 6 Patterson, M. L. (1982). A Sequential Functional-Model of Nonverbal Exchange.
7 *Psychological Review*, *89*(3), 231-249. doi:Doi 10.1037/0033-295x.89.3.231
- 8 Plomp, G., Michel, C. M., & Herzog, M. H. (2010). Electrical source dynamics in three
9 functional localizer paradigms. *NeuroImage*, *53*(1), 257-267.
10 doi:10.1016/j.neuroimage.2010.06.037
- 11 Ponari, M., Trojano, L., Grossi, D., & Conson, M. (2013). "Avoiding or approaching eyes"?
12 Introversion/extraversion affects the gaze-cueing effect. *Cogn Process*, *14*(3), 293-
13 299. doi:10.1007/s10339-013-0559-z
- 14 Puce, A., Smith, A., & Allison, T. (2000). ERPs evoked by viewing facial movements. *Cognitive*
15 *Neuropsychology*, *17*(1-3), 221-239.
- 16 Regan, D. (1989). Human brain electrophysiology: evoked potentials and evoked magnetic
17 fields in science and medicine.
- 18 Robson, K. S. (1967). The role of eye-to-eye contact in maternal-infant attachment. *J Child*
19 *Psychol Psychiatry*, *8*(1), 13-25.
- 20 Rothkirch, M., Madipakkam, A. R., Rehn, E., & Sterzer, P. (2015). Making eye contact without
21 awareness. *Cognition*, *143*, 108-114. doi:10.1016/j.cognition.2015.06.012
- 22 Rotshtein, P., Richardson, M. P., Winston, J. S., Kiebel, S. J., Vuilleumier, P., Eimer, M., . . .
23 Dolan, R. J. J. H. b. m. (2010). Amygdala damage affects event-related potentials for
24 fearful faces at specific time windows. *31*(7), 1089-1105.

- 1 Sagiv, N., & Bentin, S. (2001). Structural encoding of human and schematic faces: holistic and
2 part-based processes. *J Cogn Neurosci*, *13*(7), 937-951.
3 doi:10.1162/089892901753165854
- 4 Schulze, L., Renneberg, B., & Lobmaier, J. S. (2013). Gaze perception in social anxiety and
5 social anxiety disorder. *Frontiers in Human Neuroscience*, *7*, 872.
6 doi:10.3389/fnhum.2013.00872
- 7 Schweinberger, S. R., Kloth, N., & Jenkins, R. (2007). Are you looking at me? Neural
8 correlates of gaze adaptation. *NeuroReport*, *18*(7), 693-696.
- 9 Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding
10 recognition from the use of visual information. *Psychol Sci*, *13*(5), 402-409.
11 doi:10.1111/1467-9280.00472
- 12 Schyns, P. G., Petro, L. S., & Smith, M. L. (2007). Dynamics of visual information integration in
13 the brain for categorizing facial expressions. *Curr Biol*, *17*(18), 1580-1585.
14 doi:10.1016/j.cub.2007.08.048
- 15 Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. *Visual*
16 *Cognition*, *12*(1), 127-144. doi:10.1080/13506280444000157
- 17 Senju, A., & Hasegawa, T. (2006). Do the upright eyes have it? *Psychon Bull Rev*, *13*(2), 223-
18 228.
- 19 Senju, A., & Johnson, M. H. (2009). The eye contact effect: mechanisms and development.
20 *Trends Cogn Sci*, *13*(3), 127-134. doi:10.1016/j.tics.2008.11.009
- 21 Spezio, M. L., Huang, P. Y., Castelli, F., & Adolphs, R. (2007). Amygdala damage impairs eye
22 contact during conversations with real people. *J Neurosci*, *27*(15), 3994-3997.
23 doi:10.1523/JNEUROSCI.3789-06.2007

- 1 Stein, T., Senju, A., Peelen, M. V., & Sterzer, P. (2011). Eye contact facilitates awareness of
2 faces during interocular suppression. *Cognition*, *119*(2), 307-311.
3 doi:10.1016/j.cognition.2011.01.008
- 4 Sterzer, P., Stein, T., Ludwig, K., Rothkirch, M., & Hesselmann, G. (2014). Neural processing
5 of visual information under interocular suppression: a critical review. *Front Psychol*,
6 *5*, 453. doi:10.3389/fpsyg.2014.00453
- 7 Taylor, M. J., Itier, R. J., Allison, T., & Edmonds, G. E. (2001). Direction of gaze effects on early
8 face processing: eyes-only versus full faces. *Brain Res Cogn Brain Res*, *10*(3), 333-340.
- 9 Theeuwes, J. (1992). Perceptual selectivity for color and form. *Percept Psychophys*, *51*(6),
10 599-606.
- 11 Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica*,
12 *135*(2), 77-99. doi:10.1016/j.actpsy.2010.02.006
- 13 Tye, C., Mercure, E., Ashwood, K. L., Azadi, B., Asherson, P., Johnson, M. H., . . . McLoughlin,
14 G. J. D. c. n. (2013). Neurophysiological responses to faces and gaze direction
15 differentiate children with ASD, ADHD and ASD+ ADHD. *5*, 71-85.
- 16 von Grünau, M., & Anston, C. (1995). The detection of gaze direction: A stare-in-the-crowd
17 effect. *Perception*, *24*(11), 1297-1313.
- 18 Vuilleumier, P., George, N., Lister, V., Armony, J., & Driver, J. (2005). Effects of perceived
19 mutual gaze and gender on face processing and recognition memory. *Visual*
20 *Cognition*, *12*(1), 85-101. doi:10.1080/13506280444000120
- 21 Watanabe, S., Miki, K., & Kakigi, R. (2002). Gaze direction affects face perception in humans.
22 *Neurosci Lett*, *325*(3), 163-166.

- 1 Wicker, B., Perrett, D. I., Baron-Cohen, S., & Decety, J. (2003). Being the target of another's
2 emotion: a PET study. *Neuropsychologia*, *41*(2), 139-146. doi:Pii S0028-
3 3932(02)00144-6
4 Doi 10.1016/S0028-3932(02)00144-6
- 5 Willis, M. L., Palermo, R., & Burke, D. (2011). Social Judgments Are Influenced by Both Facial
6 Expression and Direction of Eye Gaze. *Social cognition*, *29*(4), 415-429. doi:DOI
7 10.1521/soco.2011.29.4.415
- 8 Yamaguchi, M. K., Hirukawa, T., & Kanazawa, S. (1995). Judgment of gender through facial
9 parts. *Perception*, *24*(5), 563-575. doi:10.1068/p240563
- 10 Yokoyama, T., Ishibashi, K., Hongoh, Y., & Kita, S. (2011). Attentional capture by change in
11 direct gaze. *Perception*, *40*(7), 785-797. doi:10.1068/p7003
- 12 Yokoyama, T., Noguchi, Y., & Kita, S. (2013). Unconscious processing of direct gaze: evidence
13 from an ERP study. *Neuropsychologia*, *51*(7), 1161-1168.
14 doi:10.1016/j.neuropsychologia.2013.04.002
- 15 Yokoyama, T., Sakai, H., Noguchi, Y., & Kita, S. (2014). Perception of direct gaze does not
16 require focus of attention. *Scientific reports*, *4*.
- 17 Zhao, M., & Hayward, W. G. (2010). Holistic processing underlies gender judgments of faces.
18 *Attention, Perception & Psychophysics*, *72*(3), 591-596. doi:10.3758/APP.72.3.591
19