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### RESEARCH REPORT

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# A frontoparietal network for volitional control of gaze following

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### Abstract

Gaze following is a major element of non-verbal communication and important for successful social interactions. Human gaze following is a fast and almost reflex-like behaviour, yet it can be volitionally controlled and suppressed to some extent if inappropriate or unnecessary, given the social context. In order to identify the neural basis of the cognitive control of gaze following, we carried out an event-related fMRI experiment, in which human subjects' eye movements were tracked while they were exposed to gaze cues in two distinct contexts: A baseline gaze following condition in which subjects were instructed to use gaze cues to shift their attention to a gazed-at spatial target and a control condition in which the subjects were required to ignore the gaze cue and instead to shift their attention to a distinct spatial target to be selected based on a colour mapping rule, requiring the suppression of gaze following. We could identify a suppression-related blood-oxygen-level-dependent (BOLD) response in a frontoparietal network comprising dorsolateral prefrontal cortex (dlPFC), orbitofrontal cortex (OFC), the anterior insula, precuneus, and posterior parietal cortex (PPC). These findings suggest that overexcitation of frontoparietal circuits in turn suppressing the gaze following patch might be a potential cause of gaze following deficits in clinical populations.

### **KEYWORDS**

cognitive control, eye tracking, frontoparietal network, gaze following, gaze following patch, social cognition

# **1** | INTRODUCTION

Humans have developed a complex communication system based on information provided by the face and the eyes (Andrew, 1963; Emery, 2000; Kobayashi & Kohshima, 1997). Prompted by the other's gaze direction, determined by the direction of the eyes and the head, human observers shift their focus of attention to the object of interest for the other, thereby establishing joint attention. This ability is one of the central

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**Abbreviations:** BOLD, blood-oxygen-level-dependent; dlPFC, dorsolateral prefrontal cortex; OFC, orbitofrontal cortex; PPC, posterior parietal cortex; GFP, gaze following patch; pSTS, posterior superior temporal sulcus; ACC, anterior cingulate cortex; IPS, intraparietal sulcus; CO, cingulo-opercular; FP, frontoparietal.

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communication channels that allow the observer to attribute her/his own object related mindset to the other, thereby establishing a Theory of (the other's) Mind (Baron-Cohen, 1994, 1995; Emery, 2000; Langton et al., 2000; Perrett & Emery, 1994).

Gaze following is a fast and quasi reflex-like behaviour that emerges very early during ontogeny (Batki et al., 2000; Del Bianco et al., 2019; Driver et al., 1999; Friesen & Kingstone, 1998; Hood et al., 1998; Langton et al., 2000; Szufnarowska et al., 2014), hence meeting Fodor's criteria of a domain specific, probably largely innate capacity (Fodor, 1983). Although gaze following is an automatic behaviour in some contexts, triggering a reflexive saccade in the observer (Feng & Zhang, 2014), observers are able to control it if alternative behaviours might be more pertinent in a given moment. For instance, following the other's gaze to her/his object of desire would be highly inappropriate if all of a sudden something dangerous appeared on the scene, requiring the observer's full attention. However, not only the significance of competing stimuli may affect gaze following behaviour but also the other's identity and the affective links between the two agents. For instance, as shown by Liuzza et al. (2011), observers are more poised to follow the gaze of their favourite political leader than the gaze of the representative of an opposing party. Other studies have shown that gaze following behaviour can be modulated by other socio-cognitive variables such as beliefs about the minds of others (Teufel et al., 2010; Wykowska et al., 2014), social status (Dalmaso et al., 2012), familiarity (Deaner et al., 2007), emotional expressions (Liuzza et al., 2011; Matsunaka & Hiraki, 2019), and even face age (Ciardo et al., 2014). Hence, gaze following is embedded into a broader behavioural context and can only be understood if we learn how pertinent contextual information is integrated (Astor et al., 2021; Ristic & Kingstone, 2005).

The generation and volitional control of reflexive saccades evoked by exogenous cues is known to recruit prefrontal and parietal structures in both human and nonhuman primates (Hanes & Schall, 1996; Munoz & Everling, 2004; Schall & Hanes, 1993; Thier & Andersen, 1998). Are these structures also involved in the volitional control of saccades triggered by the other's gaze, a feat that is much more demanding (Marino et al., 2015)? Actually, not only the control effort differs between saccades elicited by gaze and those by elementary spatial cues. Also, their neural underpinnings exhibit profound differences as outlined below.

At a perceptual level, there are many studies showing that the primate brain differentially processes social stimuli such as faces as compared with non-social symbolic cues such as arrows to empower highly complex social

interactions (Deen et al., 2015, 2020; Pitcher et al., 2019; Pitcher & Ungerleider, 2021; Sliwinska & Pitcher, 2018). Studies have also shown that the neural networks underlying shifts of attention triggered by social stimuli such as other's gaze are not identical to those involved in shifts of attention by symbolic cues (Callejas et al., 2014). For example, using Posner-like cueing paradigms, it has been shown that areas in the occipitotemporal cortex, such as the posterior superior temporal sulcus (pSTS) are more sensitive to gaze- versus arrow-triggered shifts of attention (Hooker et al., 2003; Kingstone et al., 2004). Finally, patients with specific lesions to their superior temporal gyrus or amygdala have shown only deficits in gaze-triggered shifts of attention and not of attention guided by pointing arrows (Akiyama et al., 2007; Akiyama, Kato, Muramatsu, Saito, Nakachi, & Kashima, 2006; Akiyama, Kato, Muramatsu, Saito, Umeda, & Kashima, 2006). All in all these studies suggest that there is a highly specialized system for gaze following. Yet most of the previous studies have ignored the question if the implicated system is able to accommodate two key features of gaze following, first the fact that it is "geometrical," meaning that the observer's gaze is attracted to distinct locations in 3D space and, second, that it may be subject to context dependent modulation. More recent studies on humans and monkeys have suggested that both features of primate gaze following might be underpinned by a patch of cerebral cortex (the "gaze following patch," GFP) in the posterior superior temporal sulcus (STS) (Marquardt et al., 2017; Ramezanpour et al., 2021; Ramezanpour & Thier, 2020) of monkeys and humans involved in coding the location of the spatial targets someone else is looking at in a context dependent manner (Hoffman & Haxby, 2000; Kraemer et al., 2020; Marquardt et al., 2017; Materna et al., 2008). The location and functionality of the GFP is different than its neighbouring areas involved in the control of attention based on more elementary non-social cues such as motion or colour (Bogadhi et al., 2018, 2019; Sani et al., 2021; Stemmann & Freiwald, 2019). Hence, one might also expect differences in the respective architecture involved in the cognitive control of gaze following in comparison to those mediating executive control of reflexive saccades based on more elementary symbolic cues.

In this study, we addressed the hypothesis that the volitional control of gaze following demanded by specific behavioural requirements may be a consequence of frontoparietal control of the GFP. To this end, we performed an event-related fMRI experiment in which human subjects' eye movements were tracked. This experiment allowed us to compare activation patterns evoked by gaze following and its rule-based suppression.

### 2 | METHODS

### 2.1 | Subjects

Twenty subjects (10 females, 10 males) participated in our study. This sample size was chosen without a prior power analysis and solely based on a previously published study (Marquardt et al., 2017) in which we could successfully replicate localizing the brain areas selectively responding to faces and also find the gaze following patch with large effect size and high statistical power (effect size:  $\sigma = 0.78$ , power:  $P_{(FDR-corrected)} = 0.75$ ,  $\alpha$ -level = 0.05). Subjects were between 20 and 32 years old, right-handed, and had normal or corrected-tonormal (lenses) vision. This sample size was chosen based on our previous work on the same topic using similar paradigms (Marquardt et al., 2017). The study was approved by the Ethics Review Board of the Tübingen Medical School and complied with the guidelines of the Declaration of Helsinki. All subjects received oral and written information and provided written consent to participate in our study.

# 2.2 | Paradigm

The images presenting gaze stimuli were the same as used by Marquardt et al. (2017). They were portrait photographs of a white, Caucasian female ("sender") and manipulated using Adobe Photoshop 7.0. The portrait shown in the fixation period of a trial was the female face ("fixation portrait") in front of a random pattern background (grey and black dots) with her eyes straight ahead EIN European Journal of Neuroscience FENS

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and a green iris (Figure 1). In front of her were five targets  $(3.5^{\circ} \times 7^{\circ} \text{ visual angle})$ , all the same in size and shape, but each with a different colour (from left to right: dark blue, light blue, green, light brown, dark brown). The visual angle between the targets was 12.5° for the sender portrait. For the subsequent spatial cue epoch, the portrait was manipulated in two ways: First, the eye gaze direction changed to hit one of the five targets in each trial. Second, the colour of the eyes was changed, simultaneously with the gaze direction, to match one of the outer targets' colour: dark blue, light blue, light brown, dark brown. The eye colour could also stay green, corresponding to the central green target in that trial. In our experiment, subjects were instructed to perform two different tasks. In "gaze following trials," subjects were asked to execute a saccade to the target the portrait was looking at, ignoring the colour of the iris. In "colour mapping trial," subjects were conversely asked to perform a saccade to the target corresponding to the colour of the iris of the sender, this time ignoring the direction of the eyes.

Gaze following and colour mapping trials were presented in a pseudo-randomized manner, allowing no more than three consecutive trials chosen from the same condition. At the beginning of each trial, a written rule was provided to inform the subjects about the upcoming condition (Figure 1). Subjects did not receive any explicit feedback at the end of trials on whether their response were correct or erroneous.

Between subsequent trials, there was a randomly varying interval of 14-15 s in which only the red fixation point (dimension:  $0.3^{\circ}$ ) was presented on the otherwise black screen. The long intertrial intervals were chosen to minimize the spillover of blood-oxygen-level-dependent



**FIGURE 1** Sequence of events in a trial. A trial started with the presentation of the instruction specifying which rule to apply in order to identify the target in the upcoming trial. Following a further delay of 1–5 s, a neutral portrait appeared (portrait fixation), stayed on for 5 s, and then was replaced by the spatial cue portrait. In the spatial cue period, the actor was gazing at one of the targets. Moreover, the colour of the iris changed such as to match the colour of one of the objects. One second later, the fixation point disappeared, serving as go signal to perform a targeting saccade. The consecutive trial started after an intertrial period of 14–15 s. The white dashed lines, pointing to the target depending on the task rule, were invisible to subjects during the experiments.

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(BOLD) responses from a preceding trial on a given trial. Subjects were asked to keep their eyes fixating on the red fixation point whenever visible. A trial started with the presentation of the written rule, followed by the onset of the fixation point. After a delay of 1-5 s, the neutral portrait appeared for 5 s (the portrait fixation period in Figure 1), followed by the spatial cue, available for 4 s. The red fixation point was constantly on until 1 s after the appearance of the spatial cue. The offset of the fixation point was the go-signal for subjects to make a saccade to the spatial target identified by the conjunction of the spatial information provided by the sender portrait and the specified rule (i.e., gaze following vs. colour mapping). Each subject performed 90 trials (45 trials for each task).

#### 2.3 fMRI recording

Prior to the fMRI experiment, subjects completed a training session involving the behavioural paradigms discussed before. The session took place in a darkened room and lasted approximately 45 min. Participants were seated on a comfortable chair in front of a screen (distance: 90 cm, dimension:  $120 \text{ cm} \times 80 \text{ cm}$ , size of images presented:  $40 \text{ cm} \times 30 \text{ cm}$  projected from the back by a beamer) and were asked to rest their head in a chin rest to prevent head movement.

Scanning took place 1–5 days later. Subjects lay supine in the MRI scanner, and their heads were fixed by foam rubber to minimize head movements. Visual stimuli (dimension: 45 cm  $\times$  34 cm) were backprojected on a translucent screen positioned behind the subject and seen via a mirror attached to the head coil. The resulting viewing distance between observer and image was 102 cm. Images were acquired by a 3-Tesla MRI scanner (Prisma, Siemens, Erlangen, Germany) using a 12 channel head coil (acquisition matrix:  $64 \times 64$ ). A volume of approximately 1200 T2-weighted echo-planar (epifid) images (TR: 3000 ms, TE: 35 ms, TA: 2.93 s, flip angle: 90°) was taken. The images covered the whole brain (44 transverse slices, slice order: [44:-1:1], slice thickness: 2.5 mm, gap: 0.5 mm, pixel spacing: 3 mm  $\times$  3 mm). Additionally, anatomical T1-weighted images were taken for each subject, using a magnetization prepared, rapid acquisition gradient-echo sequence (mprage) (TE: 2.96 ms, TR: 2300 ms, TI: 1100 ms, flip angle: 8°, voxel size: 1.0 mm  $\times$  1.0 mm  $\times$  1.0 mm).

Vertical and horizontal eye movements were recorded during both training and scanning sessions. Eye position recordings during training were acquired using a Cronos Vision C-ET video eye tracker. During scanning, we deployed a certificated, MRI-compatible eye-tracker

(SMI iView X<sup>TM</sup> MRI-LR; sampling rate of 60 Hz). Calibration of the eye-tracker output was performed three times during the experiment. To this end, subjects had to alter fixation between nine positions on the screen, allowing the comparison of known spatial position and tracker output.

#### 2.4 Data analysis

The whole stack of images of each subject was preprocessed and analysed deploying the SPM8 statistic parametric mapping software: (Welcome Department of Cognitive Neurology, London, UK, http://www.fil.ion. ucl.ac.uk/spm/).

For preprocessing, functional images were first realigned and slice time corrected. Anatomical images, mean image, and functional images were coregistered to enlarge mutual information. Anatomical images were segmented using templates provided by SPM (T1.nii) and used to normalize functional images. Finally, functional images were spatially smoothed using a full-width halfmaximum Gaussian filter (FWHM: 6 mm).

Data analysis was performed by modelling the events of the two tasks (gaze following and colour mapping) with a canonical hemodynamic response function and applying the general linear model (GLM). As onset times, we used the appearance of the portrait serving as baseline (the portrait fixation in Figure 1) as well as the appearance of the portrait serving as spatial cue. Regressors representing estimated head movements (translation and rotation with six degrees of freedom) were added to the model as covariates of no interest to reduce the influence of head movements during scanning. In order to eliminate slow, not task related fluctuations/changes, the BOLD response was high passed filtered (cut off frequency 1/128 Hz). For each subject, four contrasts were calculated: Gaze following versus colour mapping aligned to the onset of fixation and spatial cue, as well as colour mapping versus gaze following aligned to the onset of fixation and spatial cue. Significant changes were assessed using *t*-statistics.

In order to establish the response pattern for the group of subjects, single-subject contrasts were analysed on a second level using a random effects model that compared the average activation for a given voxel with the variability of that activation in the examined population (Friston, 1995; Friston et al., 1994). BOLD responses were considered significant and reported if the statistical significance exceeded p < 0.01, false discovery rate (FDR) corrected, at the level of single voxels and, moreover, involved clusters of more than 20 neighbouring voxels. Finally, to optimally visualize and

quantize the cortical representations, statistical *t*-maps were projected onto inflated reconstructions of cortical surface grey matter using SPM 12 (http://www.fil.ion.ucl.ac.uk/spm/).

We reasoned that the neural state representing the preparatory rule to suppress gaze following and to match colours should be established before the actual spatial cue would become available in order to initiate the suppression of a reflexive gaze following response in time. Therefore, we looked at the BOLD responses in a time window of 5-s duration, aligned to the onset of the portrait fixation (see Figure 1).

### 3 | RESULTS

### 3.1 | Behavioural performance

Eve data were available for 19 out of 20 subjects, allowing us to assess the percentage of correct target-directed saccades and the measurement of their latencies relative to the disappearance of the red fixation point. We used the time of peak saccade velocity as a proxy of saccade onset. Although this measure certainly overestimated saccade onset times, it had the advantage of substantially reduced variance. In order to exclude predictive saccades, not necessarily driven by the spatial information provided by the paradigm, we excluded saccades with reaction times less than 200 ms. There was no significant difference (Wilcoxon sign-rank test, p > 0.05) between the two conditions, neither for the percentage of correct saccadic choices (gaze following:  $85.55 \pm 2.65$  [mean  $\pm$  standard error]; colour mapping:  $81.68 \pm 23.3$  [mean  $\pm$  standard error]) nor for saccadic reaction times (gaze following:  $484.4 \pm 2.07$  [mean  $\pm$  standard error]; colour mapping:  $498.5 \pm 23.3$  [mean  $\pm$  standard error]), indicating that

both tasks were experienced equally demanding (Figure 2).

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In one out of the 20 subjects, the eye position records were too noisy to allow a reliable judgment of target choices and reaction times. This subject's data were excluded from any further analysis.

### 3.2 | BOLD results

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In order to characterize neural correlates of volitional control of gaze following, we determined BOLD responses related to the rule to suppress gaze following in order to select the saccade target based on the correspondence of eye and target colour, that is, colour mapping. To this end, we performed a whole brain search for significant changes of the BOLD response in the colour mapping task in comparison with the gaze following task. A significant BOLD response related to the rule to suppress the gaze following response was found in dorsolateral prefrontal cortex (dlPFC), orbitofrontal cortex (OFC) and the anterior insula, always on the left side. We also found two clusters in the left and right posterior parietal cortex (PPC) respectively as well as in the left and the right precuneus with significantly higher BOLD responses evoked by the rule to resort to colour mapping (Figure 3). Table 1 shows the coordinates of the locations of maximal BOLD response in these clusters. Notably, rather than being confined to the rule period, the suppression related contrast in three of these clusters, namely the ones in the left dlPFC, the left parietal lobe and the right precuneus, pervaded into the subsequent spatial cue epoch at the very same locations. Furthermore, the temporal evolution of the BOLD signal for both conditions was identical as we could not find any significant difference between the time of peak of the BOLD



**FIGURE 2** Behavioural performance: There was no significant difference in behavioural performance between gaze following and colour mapping trials, neither with respect to the number of correct trials (a) (p > 0.05, Wilcoxon sign-rank test) nor with respect to the response latencies (b) (p > 0.05, Wilcoxon sign-rank test).



**FIGURE 3** BOLD response during the rule period (colour matching versus gaze following). Significant clusters for colour matching versus gaze following were found in dlPFC, OFC, anterior insula, PPC and precuneus (p < 0.01, FDR-corrected, cluster size: 20 voxels, positive cluster [yellow colour]). The same contrast showed a suppression of activity in the GFP (p < 0.05, uncorrected, negative cluster [blue colour]). Note that the statistical thresholds for activations and deactivations are not the same.

**TABLE 1** Peak MNI coordinate of areas implicated in cognitive control of gaze following (p < 0.01, FDR-corrected, cluster size: 20 voxels).

	Left	Right
dlPFC	-48 26 30	NA
OFC	-42 47 -5	NA
Anterior insula	-36 17 -10	NA
PPC	-33 -55 38	54 - 52 35
Precuneus	-3 -64 43	3 - 64 38

activity between the two conditions (p > 0.05, paired t test). However, we observed a difference in the pattern of BOLD signal between the frontal ROIs and the parietal regions. There was an early decrease in the BOLD signal relative to the instruction onset in precuneus, bilaterally, and in the right PPC during gaze following condition, and only in the right precuneus in the colour mapping condition (Figure 4a). Similarly, we found an initial suppression of the BOLD response relative to spatial cue onset in the right precuneus in the gaze following condition (Figure 4b).

Our attempt to identity the GFP based on the contrast between gaze following and colour mapping related activity failed as the measure did not pass the multiple comparisons correction (p < 0.01, FDR-corrected), arguably because of the low statistical power of the eventrelated design (Friston et al., 1999). The preparation to follow gaze in gaze following trials did not evoke a significant BOLD response (gaze following vs. colour mapping) in these prefrontal or parietal regions, neither in the rule period nor the subsequent spatial cue period, suggesting that executive control signals are only required for suppression of the gaze following and not for its initiation.

### 4 | DISCUSSION

We deployed an event-related fMRI design in an attempt to identify cortical areas exhibiting BOLD responses related to the need to suppress gaze following if not pertinent. In our experiment, the need to suppress a gaze following response was a consequence of the rule to ignore the other's gaze and instead to use the other's eye colour to shift attention to locations associated with particular eye colours based on prior learning. The rule to suppress gaze following in the portrait fixation and the spatial cue periods was associated with the build-up of a BOLD response in several areas in the frontal and parietal cortices. Previous work has delineated the GFP based on a significant contrast between gaze following and colour mapping related activity, studied in a classical block design. Our attempt to identify the GFP, resorting to the same contrast failed as the BOLD response in the GFP did not pass the multiple comparisons correction (p < 0.01, FDR-corrected). This is not unexpected as the event-related design required by our study lacks the statistical power of the block design used in previous work (Marquardt et al., 2017). Because there was no significant difference between the two conditions, neither for the percentage of correct saccadic choices nor for saccadic reaction times, the observed patterns of BOLD activation and deactivation cannot be attributed to differences in task difficulty.

The dlPFC is connected with a wide range of other neocortical areas, garnering input from any sensory modality and in turn projecting to cortical and subcortical areas orchestrating purposeful behaviour (Miller & Cohen, 2001). However, the dlPFC is anything but a structure underlying elementary sensorimotor transformations. This is clearly indicated by the numerous non-sensorimotor influences on neuronal activity in the dlPFC such as information on past events and experiences (Shimamura, 1995), expected reward (Leon & Shadlen, 1999), a priori information on object features, places of particular interest (Lebedev et al., 2004; Pochon et al., 2001), or knowledge of the value of behaviour checked against the subject's needs (Duncan et al., 1996). As the dlPFC has access to information on past events, bodily needs, and future



**FIGURE 4** Time course of the BOLD signal relative to instruction onset (a) and spatial cue onset (b). We did not find any significant difference in the time of the peak of BOLD response between gaze following and colour mapping conditions (p > 0.05, paired *t* test). Green rectangles represent the significant BOLD suppression in each condition with respect to its own baseline tested separately (p < 0.05, paired *t* test).

ambitions, it is in a position, well suited to modify the behavioural impact of sensory signals processed by the subject in a given moment, taking the longer term interests of the subject into account (Duncan et al., 1996; Nauta, 1971). It is this ability to cognitively control behaviour that frees us from the inevitability of automatic or reflex-like behaviours facilitated by powerful preformed sensorimotor pathways (Aron et al., 2004; MacDonald et al., 2000; MacLeod, 1991; Miller & Cohen, 2001; Miller et al., 2002). The need to choose a hard-learned behaviour, the mapping of eye colour onto distinct spatial positions rather than to release gaze following, an ontogenetically preformed reflex-like behaviour as demanded in our experiment is a paradigmatic manifestation of our ability to deploy cognitive control. Hence, the finding of significant BOLD response in the dlPFC, evoked when subjects had to select the target based on eye colour and to suppress following the

other's gaze is in line with the well-accepted role of the dlPFC in cognitive control which can influence the activity of temporal cortex areas such as the GFP (Ramezanpour & Fallah, 2022).

There is one caveat to the conclusion that the prefrontal BOLD responses to the colour mapping rule reflects cognitive control, namely the possibility that it may reflect the need to recall the learned association between eye colour and target colour in order to comply with the colour mapping rule. Considering the well-established role of the dlPFC, insula and OFC in working memory (Barbey et al., 2011; Gogolla, 2017; Ridderinkhof et al., 2004), a BOLD response elicited by the processing of the eye colour rule might not be too surprising in a task depending on memorized associations. Unfortunately, our paradigm does not allow us to decide between the two possible interpretations of the colour mapping related BOLD response in the three prefrontal areas. We FENS

may mention, though, that a role in accommodating working memory in the context of the colour mapping task would of course not preclude a more general role in cognitive control. In fact, the possibility that activity in dorsolateral prefrontal cortex may have more than one root has been proposed by others before (Miller & Cohen, 2001).

More recent studies agree on cognitive control not being executed by a single brain region but rather by largely not overlapping brain networks (Dosenbach et al., 2006; Marek et al., 2015). Early studies on cognitive control stressed the role of anterior cingulate cortex (ACC) besides dlPFC (Carter & van Veen, 2007; Kerns et al., 2004; MacDonald et al., 2000). A prominent model by Botvinick and colleagues that builds on these observations proposes ACC to monitor performance, to detect upcoming conflicts and to increase activity in dlPFC if needed (Botvinick et al., 2001). More recent models suggest two anatomically and functionally distinct networks in cognitive control: a frontoparietal (FP) network, consisting of dlPFC and posterior parietal cortex (PPC), especially the area around the intraparietal sulcus (IPS), and a cingulo-opercular (CO) network, including dorsal anterior cingulate and bilateral frontal opercula (Dosenbach et al., 2006; Petersen & Posner, 2012; Power et al., 2011; Yeo et al., 2011). Activity in the FP network is trial associated, suggesting control initiation as well as the consideration of specific configurations of the task, seen as an adaptive execution of control. On the other hand, activity in the CO network is interpreted as across-trial maintenance of the task-set and the overall representation of the goal, indicating a stable implementation of task mode and strategy (Dosenbach et al., 2007; Gratton et al., 2018). Notably sustained signals in the CO network are only present in cognitively demanding tasks as compared with perceptually demanding tasks (Dubis et al., 2016). Since our experimental design, an eventrelated paradigm, was in the first place aiming at detecting adaptive and transient activity elicited by the need to implement cognitive control, we were able to measure trial associated activity in the FP network, but not in the CO network, which is in line with the current hypothesis of distinct functions in cognitive control of these two networks. Furthermore, relying on the excellent behavioural performance of our subjects in both tasks, we would not consider them as cognitively demanding and therefore do not expect them to elicit strong activity in the CO network.

The parietal cortex regions, the PPC and precuneus, are known to play a central role in the integration of visual information for space perception and the spatial guidance of behaviour (Le et al., 1998; Rushworth et al., 2001; Shulman et al., 2002; Whitlock, 2017).

Specifically, many studies stress the importance of PPC in detecting unexpected or relevant stimuli attracting attention, covertly as well as overtly (Corbetta et al., 2000; Corbetta & Shulman, 2002; Fox et al., 2003), identifying the PPC as a key node in a frontoparietal network serving attention. While attention is certainly an important ingredient of cognitive control, it does not overlap with the need to process abstract rules for the guidance of control, arguably a core aspect of prefrontal contributions to executive control. Within this framework for executive control, the PPC may be seen as the structure that organizes the updating of visuospatial representations required for successful target selection as demanded by the given rule (Brass et al., 2005). More concretely, in our experiment we may assume that as a consequence of prefrontal processing of the rule to map the iris colour, the salience of the gazed at target, represented in a putative salience representation in the PPC may be decreased, while conversely, the salience of the target that matches the portrait's iris colour would be cranked up.

In our analysis, we were only able to detect activity in left prefrontal areas. Several studies have reported on asymmetries within the FP network in the sense that left and right FP networks have different patterns in timing and are related to distinct processes in cognitive control (Budisavljevic et al., 2017; Ogawa et al., 2022; Perez et al., 2022). There is a possibility that activation in the left FP network serves distinct functions such as rule and stimulus processing, target evaluation, and the decision making process itself rather than response evaluation and adjustment, which might be performed by the right FP network (Gold & Shadlen, 2007; Gratton et al., 2017). In our experiment, we were focusing on preparatory control signals before and during the decision-making process, and the activation of left FP network is in line with its role in early cue response. We add that previous works have also argued that the demands of processing a relatively simple rule, such as in our study, can be easily accommodated by core machinery in the left prefrontal cortex (Belger & Banich, 1998; Höller-Wallscheid et al., 2017) whose output is spread to both hemispheres at the level of PPC and GFP.

We also found colour mapping-related BOLD responses in the left anterior insula. This region has been previously associated with many functions including the detection of salient stimuli, which capture attention (Uddin, 2015), certainly an aspect of our paradigm. On the other hand, the close proximity of the activity to the Broca area may suggest an alternative interpretation of it, namely, a reflection of the need to extract the rule from written information provided at the beginning of a trial (Baier et al., 2011).

Finally, also the left OFC showed stronger BOLD response in trials in which gaze following had to be suppressed. Patients with lesions of the OFC are known to have symptoms, which include impulsivity, compulsive behaviours, and perseveration as manifested by deficits in reversal-learning or tasks that require response inhibition, a function attributed to the OFC. Hence, the OFC is necessary for inhibition of "pre-potent" or hardwired response tendencies (Schoenbaum et al., 2009) and the urge to follow the other's gaze could certainly be understood as an example of a pre-potent tendency. Another role previous work has attributed to the OFC is the flexible encoding of associative information by rapidly switching between different sensory representations in lower level areas (Schoenbaum et al., 2009). Hence, in the context of our experiment, the OFC might also contribute to establishing the association between iris and target according to colour information.

We should note that the frontoparietal brain areas activated during cognitive control of gaze following might not be the only areas involved in this task as we may have missed other brain regions due to the relatively low effect size and statistical power of our study (effect size:  $\sigma = 0.62$ , power:  $P_{(FDR-corrected)} = 0.56$ ,  $\alpha$ -level = 0.05) in comparison to the previous one in which we localized the gaze following patch (Marquardt et al., 2017).

We did not observe any significant difference between the average reaction times in the gaze following and colour mapping conditions. However, a close look at the reaction times distribution (Figure 2b) reveals that the gaze following reaction times do not follow an ex-Gaussian pattern typically seen in decision making tasks, suggesting that in the case of gaze following, in addition to the later Gaussian component, an earlier component might have been involved. Since gaze following and colour mapping conditions contain identical visual information and motor responses, the only possibility which can explain the difference in the shape of these two distributions might be the distinct perceptual processes underlying the decisions. In the case of gaze following, the decision threshold can be reached faster, hence, there is an additional early component in the reaction time distribution. This is in line with computational models such as Linear Approach to Threshold with Ergodic Rate (LATER) model (Noorani & Carpenter, 2016), which assumes that the decision process is linear and the response is triggered when the accumulated evidence reaches a decision threshold. Such faster rise to the decision threshold in our study, could be a consequence of a shortcut pathway, most likely through subcortical areas such as the amygdala or superior colliculus, being able

to interpret other's gaze direction to shift spatial attention, ultimately speeding up saccadic target selection. There are several experiments on monkeys supporting the existence of such a pathway and its sensitivity to facial information (Nguyen et al., 2014; Taubert et al., 2018). This notion gets further support from psychophysical experiments in monkeys using other behavioural paradigms more sensitive to capture temporal aspects of gaze following (Marciniak et al., 2015), which suggest that the early component of gaze following cannot be fully suppressed in response to cognitive control signals. Future studies are required to investigate neural substrates of early component of gaze following responses.

While there was no significant difference between the time of peak of the BOLD activity between the two conditions in the frontal and parietal regions, there was an early decrease in the BOLD signal relative to the instruction onset or spatial cue onset only in the parietal regions during gaze following condition (Figure 4), which might be due to functional differences between the frontal and parietal cognitive control systems as discussed further up.

In sum, our study suggests that a frontoparietal control network is involved in the control and supervision of gaze following by integrating contextual information for the suppression of gaze following in situations in which it may be inappropriate to follow the gaze of others. This suppression of gaze following most probably involves the generation of a veto-signal among those networks, conveyed to the GFP and other dependent cortical structures resulting in effective suppression of gaze following behaviour.

### **AUTHOR CONTRIBUTIONS**

Hamidreza Ramezanpour and Peter Thier designed the study; Maria-Sophie Breu and Peter W. Dicke collected the data. Maria-Sophie Breu and Hamidreza Ramezanpour analysed the data. Maria-Sophie Breu, Hamidreza Ramezanpour, and Peter Thier wrote the manuscript.

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### CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding authors upon reasonable request.

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### PEER REVIEW

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