Neural basis of social attention: common and distinct mechanisms for social and non-social orienting stimuli

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Running title: Neural basis of social attention.

HIGHLIGHTS

- Attentional orienting triggered by social (gaze) and non-social (arrow) cues is comparable.

- When social and non-social stimuli are used as targets, qualitatively different behavioural effects are observed.

- This study explores the neural bases of shared and dissociable neural mechanisms for social and non-social stimuli.

- Shared mechanisms were found in the functional coupling between right parieto-temporo-occipital regions.

- Dissociable mechanisms were found in the functional coupling between right FEF and ipsilateral and contralateral occipito-temporal regions.

ABSTRACT

Social and non-social directional stimuli (such as gaze and arrows, respectively) share their ability to trigger attentional processes, although the issue of whether social stimuli generate other additional (and unique) attentional effects is still under debate. In this study we used the spatial interference paradigm to explore, using functional Magnetic Resonance Imaging (fMRI), shared and dissociable brain activations produced by gaze and arrows. Results showed a common set of regions (right parieto-temporo-occipital) similarly involved in conflict resolution for gaze and arrows stimuli, which showed stronger co-activation for incongruent than congruent trials. The frontal eye field (FEF) showed stronger functional connectivity with occipital regions for congruent as compared to incongruent trials, and this effect was enhanced for gaze as compared to arrow stimuli in the right hemisphere. Moreover, spatial interference produced by incongruent (as compared to congruent) arrows was associated with increased functional coupling between the right FEF and a set of regions in the left hemisphere. This result was not observed for incongruent (as compared to congruent) gaze stimuli. The right FEF also showed greater coupling with left temporo-occipital regions for those conditions in which larger conflict was observed (arrow incongruent vs. gaze incongruent trials, and gaze congruent vs. arrow congruent trials). These findings support the view that social and non-social stimuli share some attentional mechanisms, while at the same time highlighting other differential effects.

Keywords: Attentional Orienting, Social Attention, Spatial Congruency Effect, Frontal Eye Field, Functional Connectivity.

Social attention skills are notable in humans. Gaze, head, and body orientation help us determine other people's focus of attention and intentions. Accordingly, we tend to direct our attention towards the focus of other people's attention in order to infer their goals, intentions, and actions (Nummenmaa and Calder 2009). Humans are particularly adept at perceiving and discriminating gaze direction (George and Conty 2008), and gaze following is crucial for developing some cognitive processes, such as language, theory of mind, and emotion recognition. Neuroimaging and neuropsychological evidence have unravelled an extensive neural network (referred to as the "social brain") involved in social attention, including areas related to face and gaze perception, attention, emotion, and mental state attribution (Itier and Batty 2009; Nummenmaa and Calder 2009; Hadders-Algra 2022). Although the neural network of the social brain extends over both hemispheres, right hemisphere activations are more pronounced (Freiwald et al. 2017).

Face perception and recognition involve the inferior occipital gyrus (IOG), the fusiform gyrus (FG), and the superior temporal sulcus (STS). These regions are associated with the visual analysis of different facial properties (Haxby et al. 2000; Nummenmaa et al. 2010), such as processing basic components, invariant facial aspects, and changeable facial aspects (Sato and Uono 2019). The STS has been particularly implicated in gaze perception. While the anterior part of the STS (aSTS) seems to represent gaze direction with fine-grained accuracy (Carlin and Calder 2013; Hadders-Algra 2022), the posterior part of the STS (pSTS) has been mostly associated with the interpretation of the social intention of gaze, action observation, and theory of mind (Nummenmaa and Calder 2009; Redcay et al. 2010; Pfeiffer et al. 2013; Yang et al. 2015). Apart from the perceptual processing of gaze, attention is usually

attracted to the eyes and to the location the eyes are looking at. These attentional effects have been associated with the activation of parietal regions such as the superior intraparietal sulcus and the temporo-parietal junction (TPJ) (Lockhofen et al. 2014). Following the idea that humans show an automatic tendency to follow the gaze direction of others, some studies support the idea that the pSTS region and the dorsal attention system, superior parietal lobule (SPL), and frontal eye field (FEF) are implicated in goal-directed and exogenous shifts in attention (Nummenmaa and Calder 2009). Specifically, the gaze direction effect in lateral and inferior parietal regions could reflect attentional orienting in response to gaze cues (Carlin and Calder 2013).

Numerous studies have tested the assumption that orienting of attention by eye-gaze direction, compared with other non-biological directional stimuli such as arrows, might be faster or more efficient, by comparing attentional orienting triggered eye-gaze with arrow stimuli using the spatial cueing paradigm (Friesen and Kingstone 1998; Birmingham and Kingstone 2009; Galfano et al. 2012; Heyes 2014; Capozzi and Ristic 2018). However, these studies found subtle or no behavioural differences between eye-gaze and arrow cues, leading some authors to propose that eye-gaze attentional effects are at least partially driven by a domain-general attentional process (Chacón-Candia, Román-Caballero, et al. 2023). At the neural level, when comparing attentional orienting to eye-gaze and arrow cues, some studies have observed similar activations in fronto-parietal regions (Brignani et al. 2009; Greene et al. 2009; Sato et al. 2009; Callejas et al. 2014; Zhao et al. 2017). Other studies found subtle differences in cortical activations for social as compared to non-social cues (Kingstone et al. 2004; Hietanen et al. 2006; Tipper et al. 2008; Engell et al. 2010; Ristic and Giesbrecht 2011; Lockhofen et al. 2014; Caruana et al. 2015). Increased activation of ventral regions (TPJ

and inferior parietal cortex) during attentional reorienting for invalid (spatially non-attended) eye-gaze trials as compared to invalid arrow trials has been reported (Joseph et al. 2015), suggesting that gaze direction may automatically elicit expectations regarding other people's intentions and that TPJ is activated during invalid trials to redirect attention.

As reviewed above, behavioural effects observed in spatial cueing procedures with arrow and eye-gaze cues are comparable (see Chacón-Candia, Román-Caballero, et al. 2023), and the brain activations related to orienting attention triggered by these two stimuli are partially similar (Greene et al. 2009; Sato et al. 2009; Callejas et al. 2014). However, qualitative behavioural differences when responding to arrow versus eye-gaze stimuli have recently been reported using different paradigms (Marotta et al. 2012, 2018; Gregory and Jackson 2017; Chacón-Candia, Lupiáñez, et al. 2023). Perhaps the most appropriate experimental procedure to differentiate the attentional effects of arrows and eye-gaze is the spatial interference paradigm. In this paradigm, participants had to discriminate the direction of the targets (arrows or eye-gaze), which were randomly displayed to the left or right of a central fixation point. They were instructed to press the left button when the target pointed to the left and the right button when the target pointed to the right. This paradigm is a combination of the Spatial Stroop and Simon effects, categorized as a type 7 dimensional overlap according to Kornblum et al.'s (1990) taxonomy. Specifically, during incongruent trials, there is a spatial conflict arising from stimulus-stimulus (S-S) interaction between the irrelevant stimulus location and the relevant stimulus direction (Spatial Stroop effect) (Luo and Proctor 2013; Pang et al. 2020), as well as a spatial conflict stemming from

stimulus-response (S-R) interaction between the irrelevant stimulus location and the relevant response location (Simon effect) (see Narganes-Pineda et al. 2022 as an example Simon effect using the spatial interference paradigm).

Using the spatial interference paradigm, Marotta et al. (2018) showed that eye-gaze and arrow stimuli lead to opposite spatial interference effects. Consistent with a spatial interference effect (Lu and Proctor 1995; Lupiáñez and Funes 2005), arrows elicited faster responses when their direction was congruent with their position (e.g., a left-pointing arrow presented to the left; Standard Congruency Effect; SCE) as compared to incongruent trials. Eye-gaze stimuli, on the other hand, produced faster reaction times (RTs) when their direction was incongruent with their position (e.g., a left-looking eye-gaze stimulus presented to the right) as compared to congruent trials, giving rise to the Reverse Congruence Effect (RCE). This RCE with eye-gaze stimuli have been widely replicated. (Jones 2015; Torres-Marín et al. 2017; Marotta et al. 2019; Edwards et al. 2020; Ishikawa et al. 2021; Román-Caballero et al. 2021; Narganes-Pineda et al. 2022). This dissociation provides evidence for the existence of a distinct attentional mechanism specific to eye-gaze stimuli. Moreover, in an electroencephalogram (EEG) study, Marotta et al. (2019) directly compared the temporal dynamics of the conflict processing triggered by eye-gaze and arrow stimuli. They found similar effects on earlier event-related potential (ERP) components (P1 and N1) and a dissociation between eye-gaze and arrows only on late components (N2 and P3). The results were interpreted as suggesting that spatial conflict triggered by eye-gaze and arrow stimuli is supported by both early shared and later dissociable processes.

Based on these findings, some researchers have proposed that eye-gaze stimuli trigger domain-general attentional mechanism, similar to arrow stimuli, which involves the processing of spatial dimensions and directional information. There also seems to be an additional social-specific mechanism that is potentially responsible for the occurrence of RCE with eye-gaze stimuli (Hemmerich et al. 2022; Chacón-Candia, Román-Caballero, et al. 2023). The social nature of this effect is supported by studies showing the modulation of the RCE by the emotional expression displayed on the target face (Jones 2015; Marotta et al. 2022), as well as the negative correlation between social anxiety scores and the RCE elicited by eye gaze but not the SCE elicited by arrows or words (Ishikawa et al. 2021).

The present study sought to investigate the neural mechanisms associated with the attentional mechanisms elicited by social and non-social stimuli using the spatial interference paradigm. Few neuroimaging studies have investigated the brain areas underlying congruency effects elicited by arrows, suggesting that incongruent spatial Stroop trials activate brain regions involved in attentional control, response selection, detection of response conflict and those biasing the processing toward the task relevant attribute (Peterson et al. 2002; Liu et al. 2004). These regions mainly include the dorsolateral prefrontal cortex, the anterior cingulate cortex, and inferior and posterior parietal cortex. Relevant to our study are the findings from Liu et al.'s (2004) research, where a spatial Stroop task was employed. This study reported higher activation for the incongruent than the congruent condition in regions of the inferior parietal lobe, which are associated with processing task-relevant attributes and visual attention, as well as regions in the dorsolateral prefrontal cortex (DLPFC), temporal

and occipital regions. On the other hand, Zoccatelli et al. (2010) demonstrated higher activations for the incongruent than the congruent condition in the DLPFC and anterior cingulate cortex (ACC) inferior frontal gyrus, along with regions in the left hemisphere that included the angular gyrus, intraparietal gyrus, occipito-parietal gyrus, as well as middle and inferior occipital regions. However, to our knowledge, no studies have investigated the brain areas involved in the spatial congruency effects elicited by eye-gaze are unknown.

If the congruency effects produced by gaze reflect a domain-general orienting mechanism, similar brain activations should be observed in fronto-parietal regions when responding to gaze and arrows. If, on the contrary, eye gaze attentional congruency effects reflect a social-specific mechanism, then some brain regions should demonstrate differential responses to eye gaze and arrows. In particular, the neural mechanisms involved in attention to eye-gaze cues may specially rely on brain areas involved in social cognition and mental state attribution (for a review see Adolphs, 2009), including the medial prefrontal cortex, the STS, and the right TPJ (Redcay et al. 2012; Caruana et al. 2015). Another further possibility is that eye gaze triggers both domain general and social-specific mechanisms, in which case results could show some brain regions with comparable activations for eye gaze and arrow stimuli, and some brain regions with differential responses.

We used functional Magnetic Resonance Imaging (fMRI) while participants performed a spatial interference task. Behaviourally, we expected different congruency effects for arrows and gaze stimuli (i.e. faster and/or more accurate responses for congruent than incongruent trials for arrows, and a reduced or even

reversed effect for gaze), in line with previous studies (Cañadas and Lupiáñez 2012; Jones 2015; Marotta et al. 2018; Hemmerich et al. 2022). On the neural level, our two main hypotheses were that: (1) brain regions associated with conflict resolution within the frontal and the parietal cortex would show similar congruency neural effects for arrows and gaze stimuli (for incongruent as compared to congruent stimuli) (Liu et al. 2004; Callejas et al. 2014); and (2) more ventral regions, such as the STS and right TPJ, as well as other face-selective regions (IOG and FG), should be more strongly engaged for the processing of gaze as compared to arrows, and might show a different response for congruent and incongruent trials depending on trial type (arrows vs. gaze). This result will indicate that social stimuli trigger both a domain general orienting (1) and a social-specific mechanism (2).

Three complementary functional analytic approaches were used to test these hypotheses. First, we used whole-brain contrasts to examine the overall set of regions being engaged during our functional MRI task. Second, based on previous evidence and the set of regions engaged during our task, we examined regions-of-interest (ROI) activation profiles to investigate their differential engagement for incongruent versus congruent trials in the processing of gaze and arrows. Third, pairwise functional connectivity was used to investigate the functional dynamics among key regions for social and non-social cues and congruent and incongruent trial types. Whole-brain functional connectivity analyses were used to validate pairwise functional connectivity results.

Materials and Methods

Participants

A total sample of 33 right-handed volunteers (mean age= 22.5 years, SD= 3.17 years, 7 males) from the University of Granada took part in the study. Participants reported normal or corrected-to-normal vision, normal colour perception and no neurological or psychiatric disorders. They followed all the safety requirements to undergo MRI scanning. Participants signed an informed consent form prior to their participation in the study and were informed about their right to withdraw from the experiment at any time. All participants received monetary compensation for their time and effort (10 €/h) and were naïve about the purpose of the experiment. This experiment is part of a larger research project, which has been positively evaluated by the University of Granada Ethical Committee (536/CEIH/2018), in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans.

The sample size was calculated based on the results of a previous study (which was run as a pilot for this fMRI experiment) in which the two-way interaction (Target Type x Congruency; see Methods and Results) presented a size effect of $\eta^2 p$ = 0.60 (see Experiment 1 – Explicit Task, Narganes-Pineda et al., 2022). The *WebPower* R package (Zhang et al., 2018) was used to estimate sample size a-priori for a repeated-measures ANOVA, *F*-tests, with an alpha of .05 and a power of .95 (from $\eta^2 p$ = 0.60, effect size *f* was estimated to be 1.225). A sample size of 13 participants was estimated, however, we decided to run a larger sample of 33 participants to obtain stronger statistical power for the fMRI analyses.

Data from 3 participants were excluded from further analyses due to either excessive head motion during scanning (2 participants; see *fMRI Data Analysis* section

below) or withdrawal from the study (1 participant). Thus, the final sample used in the behavioural and fMRI analyses was 30 participants (mean age= 22.5 years, SD= 3.28 years, 6 males).

Apparatus and Stimuli

Stimuli presentation, timing, and data collection were controlled using E-Prime 2.0 (Schneider et al. 2002). Stimuli were displayed on a screen (NNL, 32'', 1024 × 768, 60 Hz) located at the back of the scanner (located at 2.12 m), reflected onto a head coil-mounted mirror inside the scanner. Behavioural responses were recorded with two MRI compatible response devices, one in each hand, connected by optical fiber to an Evoke Response Pad interface box (Resonance Technology INC., http://www.mrivideo.com/). All stimuli were presented on a grey background. In each trial, a black fixation point (0.5 x 0.5º) was presented at the center of the screen. The target stimuli consisted of 0.5 x 2.6 º images of two arrows, two rectangles, and two full open or closed eyes, presented to either the left or right of the fixation point (see Figure 1). The distance from the fixation point to the center of the lateral stimulus was 1.8º. The eye stimuli were cropped from the original faces of the Karolinska Directed Emotional Faces (Lundqvist et al. 1998 - KDEF) using Adobe Photoshop CS. A neutral face model was used (AM10NES).

Procedure

The experiment consisted of 5 functional runs. Each functional run lasted for approximately 8.65 minutes. There were a total of 960 trials, 192 per run, which included all experimental conditions. The duration of the jitter fixation and the order of trial types were determined with an optimal sequencing programme designed to

maximize the efficiency of recovery of the Blood-Oxygen-Level Dependent (BOLD) response (Optseq II; https://surfer.nmr.mgh.harvard.edu/optseq/). The jitter fixation periods (with a duration varying randomly between 500-9000 ms; 35% of trials) were interleaved with the experimental trials as determined by the optimization programme. Before acquiring functional data, participants received instructions and performed a practice block of 27 trials. Visual feedback was provided during practice trials when no response or incorrect responses were detected.

The trial sequence is represented in Figure 1. Each trial started with a fixation point lasting for 500 ms. Participants were instructed to keep their eyes on the fixation point throughout the experiment. The target was then presented at the left or the right location (two arrows, two open eyes, two rectangles, or two closed eyes), for 1500 ms, with directional targets pointing/looking towards the right or the left location. All targets were randomly presented on a trial-by-trial basis, so that either open or closed eyes or pairs of arrows or rectangles could appear on each trial. Participants were instructed to respond to the direction (left or right) that the arrows were pointing at or that the eyes were looking at, by pressing the left key with the left index finger for arrows/eyes pointing to the left, and the right key with the right index finger for arrows/eyes pointing to the right, regardless of the target location. When a neutral stimulus appeared (rectangles or closed eyes, which do not indicate any direction), participants were required to press a different key with either their right or left thumb, counterbalanced between participants. Participants were instructed to respond as fast and accurately as possible within 1500 ms from stimulus onset.

According to the experimental design, trials were *congruent*, if the target pointed or looked in the same direction as its location on the screen (i.e., a target pointing to the right that was presented on the right side of the screen); *incongruent*, if the target pointed in the opposite direction to its location (i.e., a target pointing to the right that was presented on the left side of the screen); or *neutral,* when closed eyes or rectangles were presented.
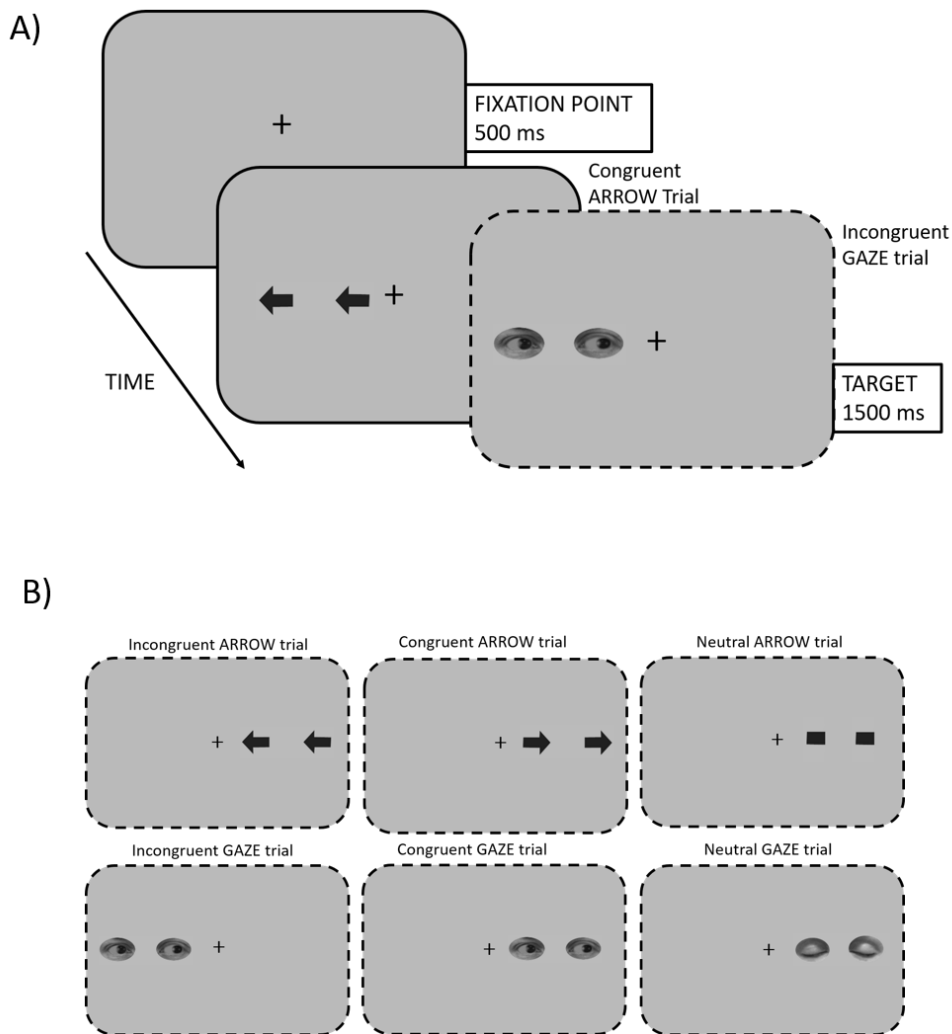

Figure 1. A) Schematic representation of the trial sequence. In the example, a congruent arrow trial is represented, together with an incongruent gaze trial. Each trial had a variable inter-trial interval (ITI) lasting between 500-9000 ms. B) Representation of congruent, incongruent and

neutral gaze and arrow stimuli. Stimuli are represented in black and white, but in the original experiment, the arrows, rectangles and the iris of gaze stimuli were depicted in brown colour.

fMRI Data Acquisition

Functional and structural images were collected on a 3-T Siemens PRISMA Fit whole-body MRI scanner at the Mind, Brain, and Behaviour Research Center (CIMCYC, University of Granada), using a 64-channel whole-head coil. Participants wore earplugs to reduce scanner noise. To limit head movement, foam padding was added between the coil and the participants' heads. In addition, participants were asked to remain as still as possible.

Functional (T2*-weighted) multiband images were acquired using the following acquisition parameters: multiband factor = 4, time-to-repetition (TR) = 1000 ms, time-to-echo (TE) = 34.80 ms, 56 interleaved 3-mm cubic axial slides, no inter-slice gap, flip angle = 56°, field of view (FoV) = 228 mm, 525 volumes per run. Prior to each functional scan, six volumes were discarded to allow for T1-equilibration effects. High-resolution T1-weighted anatomical images were also collected with the following acquisition parameters: TR = 2530 ms, TE = 2.36 ms, flip angle = 7°, slice thickness = 1 mm, FoV = 256 mm, 176 slices.

fMRI Data Analysis

Standard preprocessing routines and analyses were conducted using SPM12 (Wellcome Centre for Human Neuroimaging, London). Images were corrected for differences in slice acquisition timing and realigned to the first volume by means of rigid-body transformation. Then a partial spatial smoothing of functional images was performed using a 4 mm full width at half max (FWHM) isotropic Gaussian kernel.

After partial smoothing, the motion parameters extracted from the realignment step were used for additional motion correction algorithms implemented by the ArtRepair toolbox (Stanford Psychiatric Neuroimaging Laboratory). With this method, we were able to repair outlier volumes with sudden scan-to-scan motion exceeding 0.5 mm and/or 1.3 % variation in global intensity by linear interpolation between the nearest non-outlier time points (Mazaika et al. 2009). Participants with more than 10 % to-be-corrected outlier volumes across functional runs were excluded (i.e., 1 participant). Within each functional run, we also examined drift motion over 3 mm/degrees in translation (x, y, z) or rotation (yaw, pitch, roll) directions, excluding 1 participant who showed drift motion above this threshold. After volume repair, structural and functional volumes were coregistered and spatially normalized to T1 and echo-planar imaging templates, respectively. The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalization, the volumes were sampled to 3-mm cubic voxels. Templates were based on the MNI305 stereotaxic space (Cocosco et al., 1997). Next, functional volumes were spatially smoothed with a 7mm FWHM isotropic Gaussian kernel. Due to the quadratic relation between separate smoothing operations, the total smoothing applied to the functional data was approximately equivalent to smoothing with an 8-mm FWHM Gaussian kernel. Finally, time series were temporally filtered to eliminate contamination from slow frequency drift (high-pass filter with a cut-off period of 128 s).

Statistical analyses were performed on individual participants' data applying the general linear model (GLM). The fMRI time series data were modelled by a series of events convolved with a canonical hemodynamic response function (HRF). Six fMRI

experimental conditions (i.e., arrow congruent, arrow incongruent, arrow neutral, gaze congruent, gaze incongruent, gaze neutral) were modelled as 2s events, with each trial time-locked to the initial presentation of each stimulus. Neutral trials were initially added to the procedure for use as a baseline condition. However, comparisons of arrows>neutral and gaze>neutral demonstrated that the BOLD signal in occipito-temporal regions was increased for neutral as compared to either arrows or gaze conditions. This might be due to the fact that, although neutral, congruent and incongruent trials were equally likely to be presented (33.3%), neutral (non-directional) trials were less likely to be presented (33.33%) than directional (congruent and incongruent) trials (66.66%). Therefore, we decided to exclude neutral trials from the analyses. Anticipatory responses, trials with no responses, and trials with the incorrect key pressed were considered errors and were modelled separately and not considered in the main analysis. The produced functions were entered as covariates of interest in the GLM, together with the motion parameters for translation (x, y, and z) and rotation (yaw, pitch, and roll), which were entered as covariates of no interest. SPM12 FAST was used for temporal autocorrelation modelling in this GLM due to its optimal performance in terms of removing residual autocorrelated noise in first-level analyses (Olszowy et al. 2019). The least-squares parameter estimates of the height of the best-fitting canonical HRF for each condition were used in pairwise contrasts. Contrast images, computed on a participant-by-participant basis were submitted to group analysis. At the group level, whole-brain contrasts between All Stimuli > Null (fixation as baseline) were computed by performing one-sample t-tests on these images, treating participants as a random effect, and using a family-wise error (FWE) correction at the cluster level with a voxel-extent threshold of $p < .001$. All coordinates

throughout the manuscript are reported in Montreal Neurological Institute (MNI) atlas space.

Regions-of-Interest (ROI) analyses were conducted with the MARSBAR toolbox of SPM12 (Brett et al., 2002) on *a priori* areas of interest typically observed in functional studies of gaze processing, attentional processing, and cognitive control. ROIs consisted of significantly active voxels identified from the All Stimuli > Fixation whole-brain functional contrast (cluster-wise FWE corrected, voxel-extent threshold of p < .001) across all participants within specific MARSBAR anatomical ROIs. This ROI definition allows us to I) define functional regions that were actually engaged by our experimental design based on a functional contrast (i.e., All Stimuli > Fixation) that is not biased for any of the study conditions, and II) make sure that those functional voxels were circumscribed to the *a priori* anatomical regions of interest. The set of defined ROIs used for ROI and functional connectivity analyses included (the centre of mass and the volume in mm^3 are indicated between parentheses): bilateral FEF (left: -22.3, -2.78, 66; 3584 mm^3, right: 28.8, -4.88, 62.8; 2280 mm^3), bilateral FG (left: -33.5, -59.5, -16.4; 9056 mm^3, right: 34.4, -59.3,-16; 7292 mm^3), bilateral IOG (left: -37.4, -76.8, -8.83; 5400 mm^3, right: 38.4, -78, -9.45; 4144 mm^3), bilateral inferior parietal lobe (IPL; left: -41, -41.7, 46.1; 11088 mm^3, right: 38.4, -44.6, 49.6; 3736 mm^3), bilateral SPL (left: -24.6, -56.6, 58.8; 9760 mm^3, right: 26.6, -56.4, 60; 8008 mm^3), right angular gyrus (31.3, -59.1, 44.5; 1272 mm^3), right supramarginal gyrus (42.2, -35.9, 42.3; 920 mm^3), right middle and inferior temporal gyrus (MTG/ITG; 48.9, -59.9, -2.72.6; 10640 mm^3). In the All Stimuli > Fixation comparison the right STS did not show activation. However, given this comparison is an average of arrows and gaze, it is possible that this region was not activated because it is more activated for gaze than arrows. As this

region is particularly important for gaze processing, we nevertheless added it to the analyses based on previous literature (50, -47, 13; 312 mm^3; Schobert et al., 2018). For each ROI, we conducted a repeated-measures analysis of variance (ANOVA) on the parameter estimates values, with Target type and Congruency as factors. Outlier values outside the upper (75% + 1.5 IQR) or lower (25% - 1.5 IQR) quartiles in each condition were removed from the analysis (Goss-Sampson 2022).

Finally, we examined functional connectivity via the beta-series correlation method (Rissman et al. 2004) implemented in SPM12 with custom MATLAB scripts. The canonical HRF in SPM was fit to each trial from each experimental condition, and the resulting parameter estimates (i.e., beta values) were sorted according to the study conditions of interest (arrow congruent, arrow incongruent, gaze congruent, gaze incongruent) to produce a condition-specific beta series for each voxel. Two different functional connectivity analyses were performed: 1) intra-hemisphere pairwise functional connectivity, and 2) whole-brain functional connectivity using right FEF as the seed region (see Results section).

For pairwise functional connectivity analyses, we first calculated beta-series correlation values for each ROI at the participant level. Next, we examined interactions in pairwise functional connectivity between pairs of ROIs within the same hemisphere. We decided not to explore coactivation between hemispheres to reduce the number of comparisons. Because correlation coefficients are inherently restricted to the range from − 1 to + 1, an arc-hyperbolic tangent transform was applied to these beta-series correlation r-values to make the null hypothesis sampling distribution approach that of the normal distribution (Fisher 1922). These Fisher's z normally distributed values were then submitted to repeated-measures ANOVAs with the factors Target type and

Congruency. Outlier values outside the upper (75% + 1.5 IQR) or lower (25% - 1.5 IQR) quartiles in each condition were removed from the analysis (Goss-Sampson 2022).

For the whole-brain functional connectivity analysis, the beta series associated with the right FEF as a seed were correlated with voxels across the entire brain to produce beta-correlation images. Contrasts between beta-correlation images were also subjected to an arc-hyperbolic tangent transform to allow for statistical inference based on temporally coupled fluctuations with this region. Four comparison were performed on the resulting subject contrast images to produce group correlation contrast maps with a voxel threshold extent of p < .001, cluster-wise FWE corrected: incongruent > congruent t-tests were separately performed for arrows and gaze stimuli, and arrow > gaze t-tests were separately performed for congruent and incongruent trials.

Data are available in the Open Science Framework repository (https://osf.io/y8qsu/?view_only=9b7832d63a554990bd927b817c33bc71).

Results

Behavioural Results

Following Marotta et al. (2018), trials with incorrect responses (3.27%), anticipatory responses (0.21%), and correct response trials with RTs faster than 200 ms (0.88%) or slower than 1300 ms (0.53%) were excluded from RT analysis.

Mean RTs and percentages of errors for each experimental condition are shown in Table 1. Mean RT data were submitted to 2 (Target Type: eyes and arrow) × 2 (Congruency: congruent and incongruent) repeated measures ANOVA.

Table 1. Mean correct RTs (in ms) and percentage of incorrect responses (IR) (with their corresponding standard deviations, -SD-) for each experimental condition.

	Gaze				Arrow				
	RT	SD	%IR	SD	RT	SD	%IR	SD	
Congruent	679	77	2.51	2.26	586	64	0.80	0.95	
Incongruent	674	75	3.42	3.03	612	70	1.45	1.62	

The analysis of the mean RTs revealed a main effect of Target Type, $F(1,29)= 230.74$, MSE= 784, $p<0.001$, $\eta^2 p = 0.89$, with shorter RTs for arrow (599 ms) than for gaze targets (676 ms). The main effect of Congruency was also significant, $F(1,29)= 6.74$, MSE= 553, $p<0.015$, $\eta^2 p = 0.19$, with shorter RTs for congruent (633 ms) than for incongruent trials (642 ms). The crucial Target Type x Congruency interaction was significant, $F(1,29)= 30.12$, MSE= 236, $p<0.001$, $\eta^2 p = 0.51$. Planned comparisons showed that for arrow stimuli, RTs were significantly slower for incongruent (612 ms) than for congruent trials (586 ms), $F(1,29)= 47.53$, MSE=222 , $p<0.001$, $\eta^2 p =0.62$. In contrast, for gaze stimuli, no congruency effect was observed, $F<1$ (Figure 2).

The analysis of errors showed a main effect of Target Type, $F(1,29)=23.01$, $p<0.001$ $\eta^2 p=0.44$, with more errors for gaze targets (2.96%) than arrow targets (1.13%). The main effect of Congruency was also significant, $F(1,29)=12.58$, $p=0.001$ $\eta^2 p=0.30$, with more errors for incongruent (1.65%) than congruent trials (2.44%). The interaction Target type x Congruency was not significant, $F<1$.
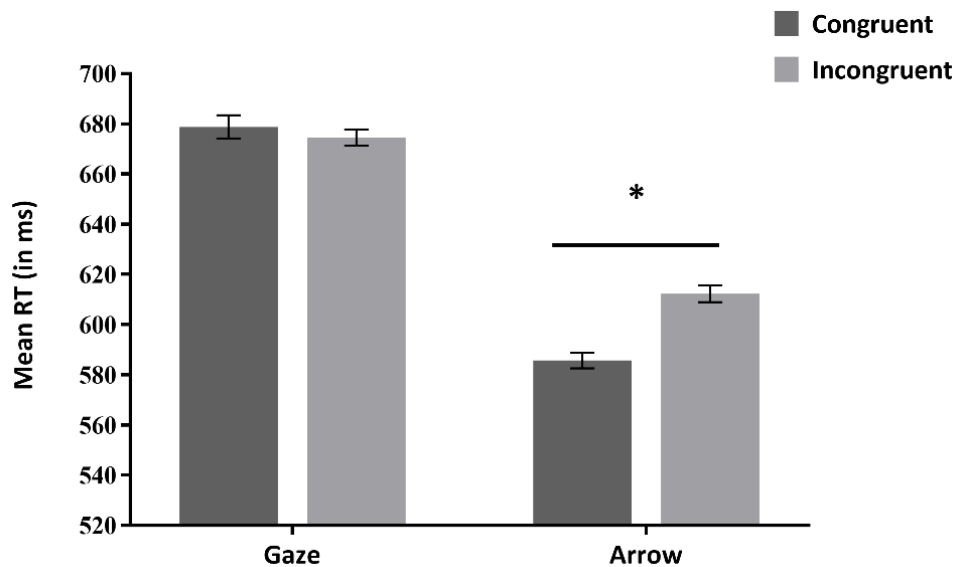
Figure 2. Mean RT for each Target Type and Congruency condition. Cousineau's method, (2005) was used to calculate the standard error of the mean represented as error bars. Asterisks denote statistically significant planned comparisons (p<0.001).

fMRI Results

The main aim of the fMRI analysis was to examine the hypotheses that there are common mechanisms for the congruency effect produced by arrows and gaze reflected in increased neural activations and/or co-activations for incongruent than congruent trials, and possible additional mechanisms associated with differential responses for congruent and incongruent trials in the processing of gaze and arrows. In addition, gaze is expected to increase brain responses in the FG, the STS, the IOG, and TPJ compared to arrows (especially in the right hemisphere).

The whole-brain contrast All Stimuli > Fixation (as baseline) revealed the regions that demonstrated larger BOLD responses when both gaze and arrow stimuli,

in congruent and incongruent conditions, were presented compared to fixation (as baseline) (see Figure 3). Next, we report first the results of ROI analyses, followed by pairwise functional connectivity analyses and whole-brain functional connectivity analyses.
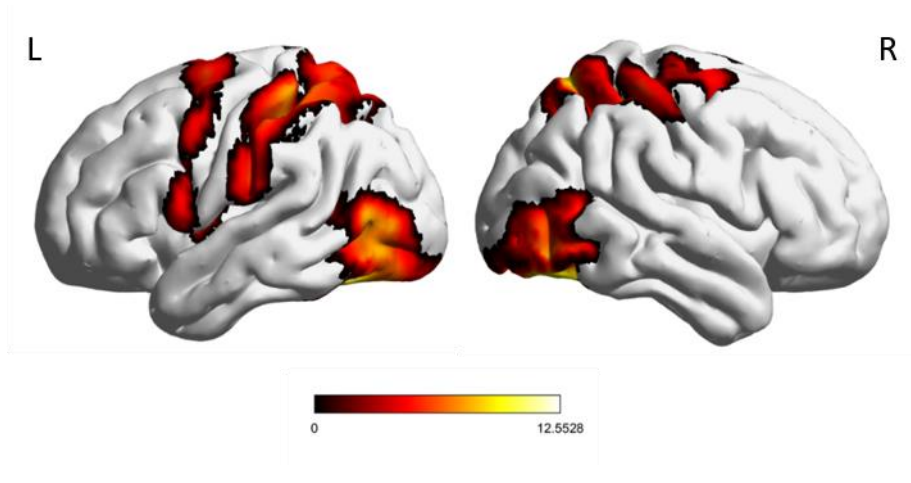

Figure 3. Brain renderings showing activations for All Stimuli > Fixation (baseline) whole-brain contrast (cluster-wise FWE corrected with a voxel-extent threshold of p < .001). The colour bar denotes t-values. L: Left hemisphere. R: Right hemisphere.

ROIs Analysis

In line with previous evidence, we selected the regions of interest (see *Methods* section) related to gaze processing, attentional processing, and cognitive control. In these regions, we found an increase in the BOLD signal in bilateral FEF, bilateral SPL and IPL, bilateral FG, and bilateral IOG. Further regions that showed increased activation in the right hemisphere only in respect to fixation (as baseline) were the angular gyrus, supramarginal gyrus, pSTS, and ITG/MTG.

The 2 (Target Type: arrows vs. gaze) x 2 (Congruency: congruent vs. incongruent) ANOVA on the ROI parameter estimates revealed a group of regions with significant main effects of Target Type and Congruency (see Table 2). All regions presented an increased % signal change for gaze compared with arrow trials, except the left IPL. Another set of regions in the left hemisphere, including the FEF, IPL, SPL, FG, and IOG, revealed a significant main effect of Congruency, with larger BOLD signal intensity for incongruent than congruent trials. In the right hemisphere, only the STS showed a main effect of Congruency, with larger % signal change for incongruent than congruent trials. The interaction Target Type by Congruency was not significant in any of the examined ROIs (ps≥0.052).

Table 2. ROIs showing significant main effects of Target Type and Congruency in the parameter estimate analysis.

Brain Area	F	MSE	p	η^2_p
Main effect of Target Type				
L FEF	22.05	0.09	<0.001	0.45
R FEF	16.55	0.12	<0.001	0.40
L SPL	8.33	0.20	0.008	0.24
R SPL	8.60	0.27	0.007	0.25
R IPL	16.82	0.20	<0.001	0.37
L FG	68.06	0.30	<0.001	0.72
R FG	106.43	0.17	<0.001	0.80
L IOG	76.82	0.22	<0.001	0.74
R IOG	149.75	0.23	<0.001	0.85
R Angular	7.13	0.20	0.013	0.21
R Supramarginal	19.25	0.12	<0.001	0.42
R MTG/ITG	24.54	0.12	<0.001	0.46
R pSTS	13.78	0.09	<0.001	0.35
Main effect of Congruency				
L FEF	11.44	0.08	0.002	0.30
L SPL	6.81	0.14	0.015	0.21
L IPL	4.67	0.12	0.041	0.16
L FG	8.07	0.12	0.009	0.24
L IOG	13.05	0.12	0.001	0.33
R pSTS	5.62	0.05	0.025	0.18

FEF, frontal eye field; FG, fusiform gyrus; IOG, inferior occipital gyrus; IPL, inferior parietal lobe; L, left; MTG/ITG, middle temporal gyrus/inferior temporal gyrus; pSTS, posterior superior temporal sulcus; R, right; SPL, superior parietal lobe.

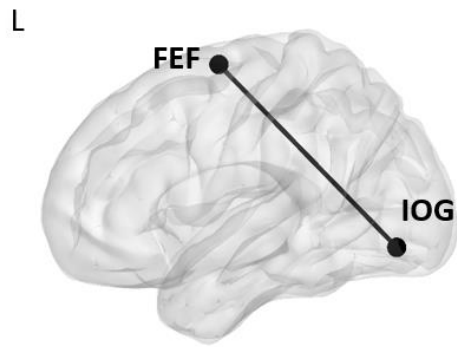### *Pairwise Functional Connectivity Analysis*

The pairwise functional connectivity analysis (2x2 ANOVA for each pair of regions of interest) revealed a main effect of congruency in the functional coupling between the left hemisphere FEF and the IOG. These regions were more strongly coupled for

congruent trials compared to incongruent trials ($F_{(1, 28)}$ =8.037, p =.008, η^2_p = .223). In the right hemisphere, two pairs of regions demonstrated a main effect of congruency, with a larger co-activation for incongruent than congruent trials: Angular gyrus with IOG ($F_{(1, 29)}$ =5.722, p =.023, η^2_p = .165) and supramarginal gyrus with ITG/MTG ($F_{(1, 27)}$ =4.437, p =.045, η^2_p = .141) (Figure 4, panel A). A further two pairs of regions in the right hemisphere (FEF-FG and FEF-IOG) demonstrated a main effect of congruency, that was, however, better explained by the interaction between Target Type x Congruency (FEF-FG, $F_{(1, 28)}$ =4.810, p =.037, η^2_p = .147; and FEF-IOG, $F_{(1, 27)}$ =4.394, p =.046, η^2_p = .140). These pairs of regions showed greater co-activations for congruent trials compared with incongruent trials for gaze stimuli (both comparisons p<.001), whereas coupling between congruent and incongruent trials was comparable for arrow stimuli (both comparisons F<1). The right FEF and right IPL also showed a significant Target Type by Congruency interaction, $F_{(1, 29)}$ =4.799, p =.037, η^2_p = .142, but planned comparisons revealed no significant differences between congruent and incongruent trials either for gaze (p=.087) or for arrows (p=.207) (Figure 4, panel B). Note that these ANOVAs did not survive correction for multiple comparisons. These pairwise functional connectivity analyses were complemented with whole-brain functional analysis (see next section).

We speculated that these results might be affected by the location of the stimuli. To explore this issue, we reanalysed the data considering stimulus location as a factor. Results showed that location did not modulate the Target Location x Target Type x Congruency interaction for any of the ROIs examined (all ps>.05), except for the right supramarginal-SPL pair of ROIs Target Location x Target Type x Congruency interaction, $F_{(1,27)}$=4.262, p =.049, η^2_p = .136). However, this interaction is difficult to

understand, as planned comparisons comparing congruent and incongruent trials for gaze and arrows in each stimulus location were not significant (all ps>.236). Therefore, we could conclude that there is not clear evidence about the location of the stimulus in
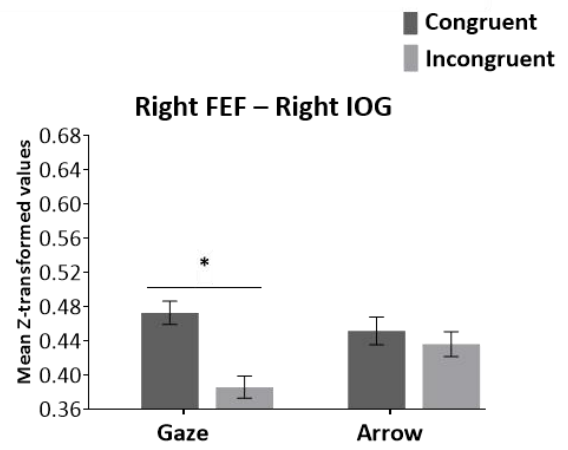
A)
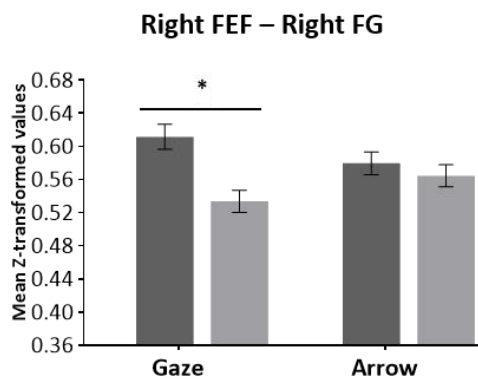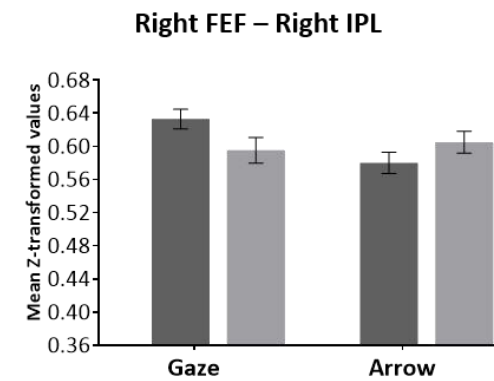

B)

C)

Right FEF – Right IOG

D)

Right FEF – Right FG

E)

Right FEF – Right IPL
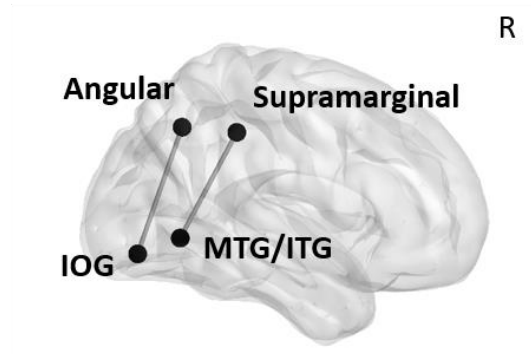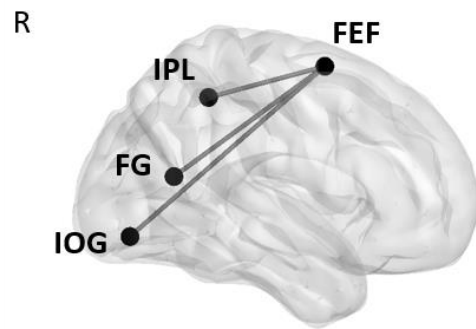
the reported results.

Figure 4. A) Representation of the pairs of regions showing a main effect of Congruency (and no Congruency x Target type interaction) in pairwise functional connectivity analysis. Black edges indicate congruent trials > incongruent trials. Grey edges indicate incongruent trials > congruent trials. L: Left hemisphere. R: Right hemisphere. B) Graphical representation of the 3 pairs of regions demonstrating a significant interaction between Target type and Congruency in pairwise functional connectivity analyses. Edges indicate that the interaction was significant in the analysis of these three pairs of regions. C-D-E) Fisher's *Z* values for the Target type by Congruency interaction in the functional coactivation between the FEF-IOG, FEF-FG, and FEF-IPL in the right hemisphere. Cousineau's method (2005) was used to calculate the standard errors of the means represented as error bars. Asterisks represent statistically significant planned comparisons (p<0.05).
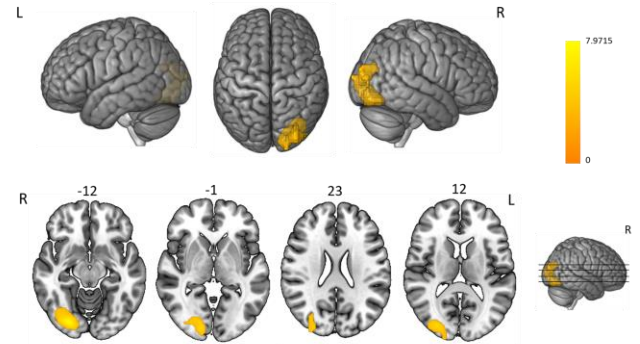

Whole-brain Functional Connectivity Analysis

Finally, a whole-brain functional connectivity analysis was performed using a seed placed in the right FEF, which demonstrated the crucial Target Type x Congruency interaction in the pairwise functional connectivity analysis with occipital, temporal, and parietal regions. This analysis was performed to ensure we had not missed potentially relevant co-activations between the right FEF and the rest of the brain in the previous ROI-based pairwise connectivity analysis. In this analysis, we first compared the whole-brain connectivity of the right FEF on arrow congruent vs. arrow incongruent trials and gaze congruent vs. gaze incongruent trials. Then we compared the whole-brain connectivity of the right FEF on arrow congruent vs. gaze congruent and arrow incongruent vs. gaze incongruent trials. The results of these comparisons are shown in Figure 5.
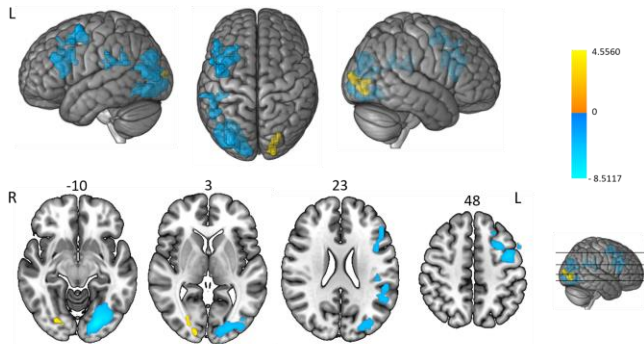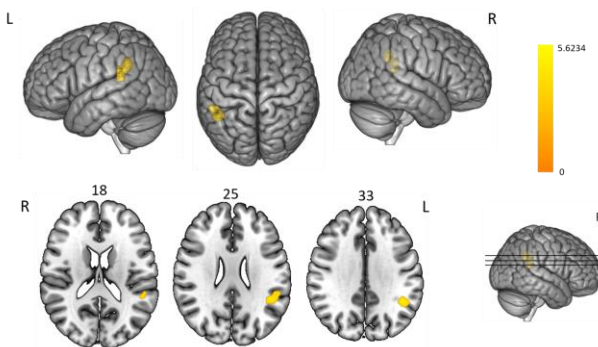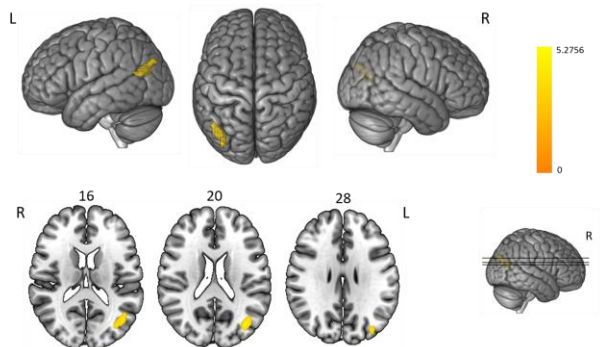
Figure 5. Whole-brain functional connectivity analysis using the right FEF as a seed for (A) arrows congruent > incongruent, (B) gaze congruent > incongruent, (C) congruent gaze > arrows, (D) incongruent arrows > gaze. The colour bars denote t-values (p < 0.001, voxel-wise FWE corrected). L: Left hemisphere. R: Right hemisphere.

Discussion

The ability of gaze following is acquired in early childhood (Hood et al. 1998; Vaidya et al. 2011) and is crucial for fruitful social interactions. When the gaze is used as a cue, responses are facilitated if stimuli are presented at the gazed-at location (Friesen and

Kingstone 1998; Driver et al. 1999; Langton and Bruce 1999; Friesen et al. 2004; Hietanen et al. 2006). Similar behavioural results have been observed with non-social stimuli that are often presented in our environment, such as arrows. Arrows orient attention to the location they are pointing at, even if they are not predictive of where targets will appear (Galfano et al., 2012; Hommel et al., 2001; Santiesteban et al., 2014; Tipples, 2002, 2008). Despite predictions that attentional orienting to gaze should be larger or more automatic than attentional orienting to arrows (Hooker et al. 2003; Friesen et al. 2004; Langdon and Smith 2005; Frischen et al. 2007), comparable behavioural effects (Chacón-Candia, Román-Caballero, et al. 2023) and highly similar brain responses (Greene et al. 2009; Sato et al. 2009; Callejas et al. 2014; Zhao et al. 2017) have been observed when gaze and arrows have been used as cues.

However, differential behavioural effects have been observed when gaze and arrows have been used as targets in the spatial interference paradigm (Cañadas and Lupiáñez 2012; Jones 2015; Torres-Marín et al. 2017; Marotta et al. 2018, 2019; Hemmerich et al. 2022; Narganes-Pineda et al. 2022). When an arrow is presented on the right, pointing right (congruent trial), responses are faster and/or more accurate than if the arrow is presented on the left, pointing right (incongruent trial) (Lupiáñez and Funes 2005). Slower responding on incongruent trials reflects the conflict created by stimuli that activate two different spatial codes, the spatial location where the stimulus is presented (irrelevant to the task) and the location the arrow points to (relevant to the task) (Luo and Proctor 2013). Interestingly, when eyes are presented as targets, congruency effects are reversed, generating the so called RCE, i.e., slower and/or less accurate responses for congruent than incongruent trials (Cañadas and Lupiáñez 2012; Marotta et al. 2018, 2019).

In this study, we examined the neural mechanisms associated with spatial conflict elicited by arrows and gaze stimuli using the spatial interference paradigm in an fMRI setting. At the behavioural level, gaze produced slower responses as compared to arrows, as expected based on previous research (Vlamings et al. 2005). This has been suggested to result from gaze producing an overall larger attentional capture due to social meaning and perceptual complexity (Hietanen et al. 2006; Marotta et al. 2018). More importantly, our behavioural results demonstrated the expected interaction between Congruency and Target type. For arrows, responses were faster for congruent than incongruent trials, demonstrating the standard congruency effect (SCE). In contrast, no significant differences were observed for congruent and incongruent gaze trials; i.e. the RCE was not significantly observed. Previous research has shown that the RCE for gaze is enhanced (only significantly observed) when the previous trial is incongruent (Hemmerich et al. 2022). Indeed, a clearly significant RCE for gaze ($F(2,58)= 37.873$, $p<.001$, $\eta^2p =0.57$) was observed in our behavioural data, when restricting the analysis to those trials that were preceded by incongruent trials. We therefore acknowledge that the lack of RCE in the present experiment might be due to the inclusion of neutral trials, which resulted in a decreased likelihood that the preceding trials were incongruent (Blais et al. 2014). Therefore, although the RCE for gaze was not overall observed in our experiment, we are confident that the paradigm performed as expected, as the congruency effect was significantly different for gaze and arrow stimuli (significant interaction between Congruency and Target type), and the RCE was observed after incongruent trials, when it is typically observed (Hemmerich et al. 2022).

At the neural level, imaging results showed an overall increase in BOLD responses for gaze versus arrow stimuli in a distributed set of fronto-parietal-temporal-occipital areas. The strong bilateral activation of FG and IOG found in the parameter estimate ROI analysis may reflect increased processing of social gaze stimuli. Indeed, in addition to their implication in facial processing (Haxby et al. 2000), the contribution of the FG and IOG to gaze perception has also been shown (Nummenmaa et al. 2010; Ethofer et al. 2011). Furthermore, our results are consistent with studies reporting that FG is more responsive to social than non-social stimuli (Kanwisher et al., 1997; Kanwisher, 2000; Tong et al., 2000). We also showed increased pSTS activation for the gaze > arrow contrast in the parameter estimate ROI analysis. This result is in line with previous results (Hooker et al. 2003; Kingstone et al. 2004) and is consistent with the view that STS is not only involved in gaze direction processing but also more generally in the processing of biologically significant stimuli (Materna et al. 2008; Carlin and Calder 2013; Yang et al. 2015).

One of the main questions that motivated our research was to explore if shared or dissociable processes support the spatial conflict triggered by gaze and arrow stimuli. We hypothesized that some brain regions associated with conflict resolution within the frontal and the parietal cortex would show similar congruency effects for arrows and gaze stimuli, while more ventral regions such as the STS and right TPJ, as well as other face-selective regions (IOG and FG), might show different congruency effects for arrows and gaze. Our results suggest that the processing of conflict resolution produced by gaze and arrow stimuli is supported by shared mechanisms but also indicate some dissociations.

A set of regions in the left hemisphere, including the FEF, IPL, SPL, FG and IOG, demonstrated larger BOLD responses for the incongruent condition relative to the congruent condition. The pSTS in the right hemisphere also demonstrated larger BOLD responses for the incongruent than the congruent condition. All these regions have previously been related to attentional orienting processes, and their comparable activation for social and non-social stimuli in our spatial interference paradigm is consistent with studies using arrow and gaze stimuli as cues in visuospatial attentional orienting tasks (Greene et al. 2009; Sato et al. 2009; Callejas et al. 2014), which showed no differences in overall BOLD activation for both stimuli. In addition, other brain regions that have been related to conflict resolution in Stroop like tasks, such as the inferior parietal lobe and temporo-occipital regions (Liu et al. 2004; Zoccatelli et al. 2010), also showed similar patterns of higher activation on incongruent than congruent trials for both arrows and gaze in our study. Thus, our results indicate a common spatial conflict resolution mechanism for social and non-social stimuli.

In accordance with these findings, the functional connectivity analyses reported here further support shared attentional mechanisms between arrow and gaze stimuli concerning spatial conflict resolutions. For both stimuli, incongruent as compared to congruent trials led to stronger coupling of regions within the ventral attentional network (the right angular and the right supramarginal gyrus) with ipsilateral temporo-occipital regions (i.e., IOG, MTG/ITG). The ventral network has been reliably related to conflict detection and attentional re-orienting (Corbetta and Shulman 2002; Kincade et al. 2005; Joseph et al. 2015), two mechanisms involved in responding to incongruent trials in the present paradigm. These findings complement functional neuroimaging evidence showing a similar activation of the ventrolateral

attention control network when gaze or other behaviourally relevant stimuli, such as arrows, are used to orient attention (Corbetta et al. 2008; Sato et al. 2009; Callejas et al. 2014). As such, this evidence implies the existence of domain-general attentional processes that respond to the directionality of the stimulus regardless of whether the stimulus is social or non-social.

However, functional connectivity analyses also showed that the processing of conflict resolution produced by gaze and arrow stimuli is also supported by dissociable mechanisms. Although in the left hemisphere, the FEF was more strongly coactivated with the IOG for congruent than incongruent trials for both arrows and gaze, an interaction with Target Type was observed in the right hemisphere. The functional coupling between the right FEF-IOG and right FEF-FG was stronger for congruent than incongruent trials for gaze stimuli but not for arrows. This could be consistent with the RCE previously observed with gaze in the literature (Marotta et al. 2018, 2019). This result was confirmed by a whole-brain functional connectivity analysis in which the seed was placed in the right FEF. For gaze stimuli, the right FEF was more strongly connected with the ipsilateral occipital cortex for congruent than incongruent trials. In contrast, for arrow stimuli, the right FEF was more strongly coupled with a distributed set of regions of the contralateral hemisphere for incongruent than congruent trials, an effect that was not at all observed for incongruent gaze stimuli. These opposing effects indicate a dissociable mechanism between arrows and gaze processing. The FEF is part of the dorsal attentional network proposed by Corbetta and colleagues (2008, 2002), whose activation has been associated with generating and maintaining endogenous signals based on current goals (Bressler et al. 2008; Vossel et al. 2014). The dorsal network sends top-down signals that bias the processing of relevant

stimulus features and locations in the sensory cortex. The FEF also activates during reorienting, with enhanced responses when targets appear at unexpected locations (Kelley et al. 2008; Torriero et al. 2019). In our data, the coactivation of the FEF with occipital regions is larger for congruent trials (e.g., when the target appears on the right, pointing right, and therefore only one side of space is relevant), than for incongruent trials (e.g., when the target appears on the right, pointing left, and therefore the two sides of space are relevant), and this effect in larger for gaze than arrow stimuli in the right hemisphere. According to Corbetta's model, the FEF biases the processing of goal-relevant stimuli and locations in the visual cortex. Although this is a common process for arrow and gaze in the left hemisphere, in the right hemisphere this process is enhanced for gaze as compared to arrows, consistent with the RCE usually observed for gaze.

Although the underlying cognitive and neural mechanisms of this RCE remain unknown, several behavioural hypotheses have been proposed to explain this effect (Marotta et al. 2018, 2019; Hemmerich et al. 2022). The first hypothesis, known as the eye contact effect (Cañadas and Lupiáñez 2012; Marotta et al. 2018), proposes that incongruent eye-gaze trials are perceived as a direct gaze (gaze towards the participant). In other words, incongruent eye-gaze conditions are looking towards the centre, at the location the participant is looking at, therefore potentially making visual contact with the participant. This fact would improve the perception of the incongruent condition as compared to the congruent condition, which is perceived as an averted gaze (Senju and Hasegawa 2005; Senju and Johnson 2009). However, this hypothesis has been refuted in an experiment comparing an implicit version of the spatial interference task in which participants responded to the color of the eyes and

arrows (blue or brown) to an explicit version in which they responded to the direction to which they pointed. Although the eye contact was the same in both tasks, the RCE was replicated in the explicit task but disappeared in the implicit task, suggesting eye contact effect could not explain RCE (see Narganes-Pineda et al. 2022). In addition, regarding the neural networks involved in processing direct gaze and our data, our neuroimaging findings do not support the eye contact hypothesis. Previous research suggests that the processing of direct gaze involves regions such as the superior temporal sulcus (STS), fusiform gyrus (FG), orbitofrontal cortex, and bilateral amygdala (Calder et al. 2002; Pelphrey et al. 2004; for a comprehensive review, see Senju and Johnson 2009; Carlin and Calder 2013). On the other hand, the processing of averted gaze requires the involvement of regions such as the STS, intraparietal sulcus, parietal cortex regions, as well as temporal regions, in conjunction with the temporoparietal junction (TPJ) (Hoffman and Haxby 2000; Grosbras et al. 2005; Itier and Batty 2009; Nummenmaa and Calder 2009). Our activations for both congruent and incongruent gaze trials were observed in clusters of parieto-temporo-occipital regions and the superior frontal cortex, which may be more closely associated with perceiving averted gaze or gaze following. The second hypothesis, the "joint attention" hypothesis (Marotta et al. 2018; Edwards et al. 2020), proposes that an incongruent gaze looks at the fixation point, where the participant is looking, creating a shared focus of attention. Thus, this hypothesis also suggests how processing incongruent gaze trials may be facilitated compared to congruent trials. In contrast, the third hypothesis, the "joint-distraction" hypothesis (Hemmerich et al. 2022), states that processing congruent trials incurs an attentional cost due to the gaze being directed away from the task, leading to gaze following and distraction.

Our neural results seems consistent with the "joint-distraction" explanation (Hemmerich et al. 2022) and the "joint attention" explanation (Marotta et al. 2018; Edwards et al. 2020) of the RCE produced by gaze.

The "joint-distraction" account of the RCE proposes that congruent gaze stimuli (e.g., eyes presented on the right, looking right) direct attention away from the display, i.e., the focus of attention, thus slowing responses. This "joint distraction" might be related to the functional connectivity of the FEF with occipital regions, associated with the selection of the relevant location, which is more pronounced for gaze than arrows in the right hemisphere. This process could be due to the social properties of gaze stimuli. As the congruent gaze stimuli divert attention away from the task in order to discover what the eyes are looking at and attending to, further processing and reorientation is required to return to the task.

Overall, the whole-brain functional connectivity analysis showed larger brain coactivation differences between responses to congruent and incongruent arrow vs. gaze stimuli. When participants saw an incongruent arrow, the right FEF coactivated with a distributed set of regions in the contralateral hemisphere. This brain response was observed when participants had to resolve the conflict generated by an incongruent arrow (e.g., presented on the right but pointing left). In contrast, incongruent gaze trials were solved without this increased coactivation with the left hemisphere.

Two possible explanations have been proposed for this dissociable mechanism we detected for resolving conflict caused by arrows and gaze: 1) Incongruent gaze trials cause less conflict because the location of the stimulus is not considered relevant for the task, and therefore, only one spatial location is prioritized (the location the

gaze is directed at) (Hommel 2004, 2019). It is important to note that some conflict was detected, as the right supramarginal and angular gyrus were more strongly connected with occipito-temporal regions for incongruent than congruent trials for both arrows and gaze. However, the conflict produced by gaze was resolved within one cerebral hemisphere. 2) According to some psychological explanations of the RCE (Marotta et al. 2018; Edwards et al. 2020), incongruent gaze trials cause less conflict because the gaze directs attention to the central fixation point, where the participant is looking at, eliciting "joint attention". Incongruent arrows, on the other hand, direct attention to the opposite hemifield. This hypothesis is consistent with the neural data observed. Incongruent arrows direct attention to the opposite hemifield, which is related to the increase in functional connectivity between the right FEF and the opposite hemisphere; while incongruent gaze direct attention to the center, not to the opposite hemifield, and therefore, the functional connection of the right FEF with the opposite hemisphere is not needed.

Note that both explanations assume that the functional connectivity of the right FEF and the opposite hemisphere reflects attention to both sides of space, while the functional connectivity of the right FEF and the ipsilateral hemisphere reflects attention to only one side of space. This assumption is based on the observation of Ramsey et al. (2016), who reported that acute neglect (in which attention is highly biased to one side of space) is characterized by increased resting state functional connectivity of the right parietal cortex with the ipsilateral hemisphere, and decreased functional connectivity with the opposite hemisphere. However, after neglect recovery (and therefore, when participants are able to attend to both hemifields), the right

parietal cortex recovered the functional connectivity with the contralateral hemisphere.

The FEF coactivated with left tempo-occipital regions (including the SMG) more strongly for incongruent arrow vs. gaze trials, and for congruent gaze vs. arrow trials. I.e., there was an increased FEF-temporo/occipital coactivation for those conditions that generated larger conflict (incongruent arrow trials and congruent gaze trials). It has been proposed that the functional connectivity between the right FEF and bilateral SMG is associated with attentional shifts, in particular, with the disengagement of attention from the current focus (Heinen et al. 2017). In the case of arrow targets, incongruent trials are those in which the irrelevant dimension (target location) activates a response that is incompatible with the required response (associated to the relevant dimension: arrow direction). This condition thus requires reorienting, slowing RTs as compared to congruent trials. Interestingly, incongruent gaze trials did not seem to require reorienting (both from the RT and the fMRI results). In turn, the right FEF increased its connectivity with left temporal regions (including the SMG) for gaze congruent as compared to arrow congruent trials. According to the "joint distraction" account, gaze congruent trials create conflict due to attracting participants' attention away from the task, therefore requiring re-orienting. This finding provides partial support for this hypothesis and warrants additional confirmation in future research.

Limitations

The results of this study should be interpreted in the context of certain limitations. First, the implementation of neutral stimuli failed, as it affected the pattern of behavioural data, hindering the observation of the RCE. However, the RCE was significant after incongruent trials (as usually observed when exploring sequential

effects, Hemmerich et al. 2022), and the neural data did show some of the expected modulations for gaze trials, indicating that, even if not behaviourally significant, gaze stimuli were producing qualitatively different congruency effects than arrows. Second, a number of factors were not controlled for, namely the contrast and luminance of the stimuli and participant eye movements. In an unpublished pilot study using a similar spatial interference task (N=38) we observed no significant differences in the number of trials in which participants broke fixation on congruent and incongruent gaze trials (W= 362, p=0.654) and arrow trials (W=278, p=0.392). However, we acknowledge that such factors may have affected our results and should be controlled for in future fMRI studies.

Conclusions

In conclusion, our results suggest that the spatial conflict elicited by gaze and arrow stimuli share some common mechanisms: increased functional connectivity of ventral attentional regions with the ipsilateral occipito-temporal cortex during incongruent compared to congruent trials, and increased functional coupling between the FEF and the ipsilateral occipital cortex during congruent as compared to incongruent trials. The latter effect was more pronounced for gaze than arrow targets in the right hemisphere. In addition, dissociable effects were also observed: incongruent arrow targets increased the functional connectivity between the right FEF and the opposite hemisphere, an effect that was not observed with gaze stimuli. Moreover, the right FEF showed larger coupling with left temporo-occipital regions for those conditions in which larger conflict was observed (arrow incongruent vs. gaze incongruent trials, and gaze congruent vs. arrow congruent trials). These results are consistent with explanations that link the RCE to processes of joint distraction on congruent trials and

joint attention on incongruent trials, linking these processes to the functional connections of the dorsal and ventral attentional networks and their interactions with face and object selective regions of the occipital and temporal cortex.

Data/code availability statement

Readers seeking access to the data and experimental materials should contact the author Cristina Narganes-Pineda (cnarganes@ugr.es or cnpinedas@gmail.com). Data is also available in the Open Science Framework repository (https://osf.io/y8qsu/?view_only=9b7832d63a554990bd927b817c33bc71).

Ethics statement

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical guidelines laid down by the University of Granada, in accordance with the ethical standards of the 1964 Declaration of Helsinki (last update: Seoul, 2008) and was part of the research project (PSI2017-84926-P) approved by the University of Granada Ethical Committee (536/CEIH/2018). Informed consent Informed consent was obtained from all individual participants included in the study.

Authorship Statement

CNP: conceptualization, investigation, methodology, formal analysis and writing—original draft. PM-P-A: responsibility of formal fMRI analysis and writing—review & editing. AM: conceptualization, methodology and writing—review & editing. JL: conceptualization, methodology, funding acquisition and writing—review & editing. ABC: conceptualization, methodology, formal analysis, writing—review & editing, funding acquisition and supervision.

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Declaration of interest

The authors have no conflict of interest to disclose.

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