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Reflexive Social Attention modulated by Social Cues: evidences from functional Magnetic Resonance Imaging (fMRI) studies

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Supplemental Materials (Experiment 2/3)

General Introduction

Visuospatial attention can be allocated to a specific region of interest by making a saccade towards it (i.e. overtly) or in the absence of any eye movement (e.g. covertly). Attentional shifts may be based on an entirely voluntary process or be automatically and involuntarily triggered by stimuli from the outer world. The attention catching power of environmental stimuli may differ according to the category they belong in. Biological stimuli with particular social valence, such for example an oriented gaze, exert a stronger influence on attentional shifts with respect to non biological stimuli even when these provide strong directional cues (e.g. arrows). The capability of gaze to orient the behaviour of another individual is fundamental to social cognition in highly social groups like human and non-human primates. This type of joint attention mechanism makes possible complex cognitive operations ranging from “mind reading” to “anticipation and understanding of intentions and behaviours of the other individuals”. Not only gaze but also pointing hands provide cues that allow one to gather information on the external world and on co-specifics. These cues may influence the behaviour of an onlooker at entirely automatic and involuntary levels. Indeed, viewing gazes or hands pointing leftwards may reduce speed and accuracy of rightward eye or hand movements even if subjects are specifically instructed to ignore the distracting gaze or pointing stimuli.

The present dissertation has two main objectives. The first objective was aimed at investigating the neural underpinning of reflexive shifts of attention triggered by social and non-social cues and the possible modulatory role of gaze and hand pointing distracters on saccadic and hand pointing responses, respectively. Behavioural studies published by our laboratory (Crostella et al., 2009) show that observing gaze or pointing movements directionally incongruent with the eye or hand movements to be performed by an onlooker delayed the actual execution of eye or hand movements. This pattern of results suggest that reflexive joint attention is mapped according to somatotopic and not only spatial frames of reference. The specific behavioral relationship between distracting and body parts found in this studies made possible data-driven exploration of the fronto-parietal network involved in body-part specific triggering of visuospatial attention during saccadic and pointing tasks.

The second objective aimed at exploring whether reflexive joint attention is modulated by the relationship between the social status of the gazing individual and the onlookers' personality. Political psychology studies indicate that choice behaviours, such as voting preferences, are strongly influenced by the voters' specific personality traits (such as for example the perceived similarity with a political Leader). We applied the gaze-cuing paradigm to individuals with known political preferences. Distracting gazes belonged to political leaders or opinion-makers of the same or opposite political party with respect to the voters. Therefore, using fMRI, we investigated whether "high-order social variables" such as political affiliation, political attitudes and perceived personological similarity modulate neural responses in the reflexive social attention circuit.

In Chapter 1, I will briefly review some notions about Covert vs. Overt visual orienting. On the basis of Corbetta and Shulman (2002) attentional models, I will distinguish between anatomical substrates of dorsal and ventral fronto-parietal attentional networks. In Chapter 2, I will consider the concept "Reflexive Joint Attention" as central core of my researches. Importantly, I will focus on the "Social Meaning" of important biological and social cues, i.e. automatically orienting to others' gaze and/or shifting the attention toward the direction indicated by a pointing hand. Finally, the neural bases of following gaze and pointing gesture will briefly introduced in the last sections of this chapter. Chapter 3 is the "leitmotiv" of my topic. The reason for a placement of reflexive shifts of attention into a theoretically "Social Somatotopy" frame will be clarified along the chapter. Thus, I will explain the importance of a "shared representation" of another person' body respect to our own body and how visuospatial attention may be modulated by social body stimuli through a "sensorimotor mirroring process" that takes place according to body-part specific reference frames. Chapter 4 is a "wide shot" of Brain Imaging Technique. For sake of simplicity, I will introduce only functional magnetic resonance imaging (fMRI) technique and basic notions relative to it, even if others toolbox such as Eye and Pointing (home made) tracking have been employed in my experiments. In Chapter 5, I will illustrate the first fMRI experiment (Cazzato et al, 2010; HBM in press) by means we demonstrated that reflexive shifts of attention triggered by social signals are coded in the fronto-parietal cortex according to effector-specific mapping rules. Finally, Chapter 6 will deal with two experiments, (the first behavioral and the second fMRI) which share the fact that human observers (voters) are more attracted by the distracting gaze of an ingroup rather than an outgroup politicians (1st experiment) and that the proneness to follow the ingroup politicians (and opinion-makers) is reflected in brain responses of particular regions of interest (ROIs) of the fronto-parietal attentional network (2nd experiment). Importantly, both studies seem to suggest that the perceived similarity between the observer and the model played a role in mediating social attention. Because the analysis are still in process, I will give some tentative conclusion resuming the results obtained by these studies. A “Future Directions” Section will describe a new project I am working on, concerning “Reflexive social attention mediated by gaze-observation: role of the perceived fairness of others induced by economic interactions”.

Chapter 1

Orienting of visuospatial attention

1.1 Covert vs. Overt visual orienting

Attention is the mental ability that allows us to adaptively select stimuli coming from the external world, specific responses among those available in our behavioral repertoire, as well as mental representations concerning space and time (Mesulam, 1999; Nobre, 2001). Therefore, shifts of visuospatial attention are fundamental for optimizing processing of places, objects, or instants in time. Thanks to saccadic eye movements that allow to process information with the maximal acuity foveal region, we are able to rapidly and efficiently explore visual world, under both naturalistic and laboratory conditions. The exploration of a visual scene occurs by means of saccadic eye movements that rapidly (in 50–70 msec) bring the fovea, the retinal region of highest acuity, and the neural machinery associated with it onto stimuli of interest. Stimuli are processed during interspersed periods of fixation that last up to 250 msec. This set of processes is defined as ‘‘overt visual orienting’’. Behaviorally relevant stimuli, however, can be attended to in the absence of exploratory saccadic eye movements. It means that the locus of attention is dissociable from eye fixation. In addition, attention can be directed toward a location either voluntarily or reflexively when a stimulus abruptly appears in the visual field. This set of processes is defined as ‘‘covert visual orienting.’’

Many researchers have found that advance knowledge of the position of an upcoming stimulus facilitates its detection even when eye movements are not allowed (Eriksen and Hoffman, 1972; Posner, 1980). For example, in a classical experiment, Posner (1984) presented a target at 7 degrees to the left or right of fixation. Before the presentation of the target, an arrow was presented at fixation pointing toward the correct target location on 80 % of the trials. On 20 % of the trials the arrow pointed toward the wrong location. Manual reaction times for the detection or discrimination of the target were faster when subjects were able to anticipate its location. It happens because the arrow (central cue) provides advance location information that can be used to bias the processing of target stimuli. Because the cue has to be interpreted and voluntarily used, this form of cueing is called ‘‘endogenous’’. The cue per se is not necessary! Similar results are obtained when subjects are asked directly to ‘‘pay attention’’ to a certain location (Berlucchi et al., 1989). A similar facilitation of stimulus processing is found when advance location information is provided as a sensory stimulus presented at the most likely stimulus location (Jonides, 1981). This form of cueing is called ‘‘exogenous’’ and strongly it depends on sensory information. The effects of spatial cueing on visual processing are not limited to the simple detection of suprathreshold visual stimuli, but extend to many other visual tasks, including threshold detection of luminance and discrimination of shape, size, color, and motion (Bashinski and Bachrach,, 1984; Downing, 1988). The widespread effect of spatial cueing on vision indicate that processes that mediate spatial selection have wide access to visual processes specialized for feature and object analysis. The enhancement in stimulus processing produced by spatial cueing, in the absence of eye movements, is thought to reflect the activation of a mechanism that shifts attention to the stimulus location before its appearance. This may facilitate stimulus analysis in two related ways: 1) visual processes could complete stimulus analysis more rapidly at the attended location, because it takes time to reorient attention to the new (unattended) stimulus location; 2) attention could more directly influence visual processes by enhancing their sensitivity at the attended location. This would explain how attention also improves sensory thresholds (Bashinski and Bachrach,, 1984).

When recording brain activity either at the whole brain level or at the level of single neurons, different types of signals will correspond to the activation of the attentional mechanism (‘‘source’’ signals) and its interaction with the visual system (‘‘site’’ signals). For example, a source signal would be associated with a shift of attention to a location and would be recorded in areas that implement the attentional mechanism and or in visual areas responsible for stimulus analysis. In visual areas, a source signal may prime visual processes to a more efficient response. Once a stimulus is presented, stimulus analysis may be enhanced by attention. This would produce a modulation of visual processing (‘‘site’’ signal) that marks the site of the interaction between source attentional signals and visual processes. Whereas source signals provide information on the organization of attention systems, site signals provide information on how sensory (or motor or cognitive) systems are affected by attention.

The discovery of a mechanism for covertly (without eye movements) directing attention to locations raises the question of its relationship to mechanisms responsible for saccadic generation. Attention and eye movements usually move synchronously and select common targets in the visual field. Shepherd and colleagues (1986), highlighted that this relationship can occur along three forms. According to the “Independence Hypothesis”, attention and eye movement generation can involve entirely different mechanisms. It means that locations could be simultaneously computed in separate spatial maps by attentional and oculomotor systems. This assumes that it should be possible to operate simultaneous shifts of attention and eye movements in opposite directions. To the opposite, the “Identity hypothesis” states that attention and eye movement generation involve the same mechanisms. It assumes that a location is encoded by the attentional mechanism in a set of motor coordinates that specify direction and amplitude and that are also used for planning a saccadic eye movement (Rizzolatti et al., 1987). Finally, the intermediate position is the “Interdependence hypothesis” that claims attention and eye movement processes share resources or computations at some stage. For example, both attention and eye movement systems may depend on an early sensory visual representation. When both systems select the same location on the representation, their performance is optimal; when different locations are to be selected by each system, their performance is impaired.

Early papers provided conflicting evidence on whether preparing an eye movement toward a location enhanced the visual processing of stimuli presented at the same location and, vice versa, whether a shift of attention facilitated oculomotor execution (Remington, 1980; Klein, 1980). Furthermore, under certain conditions attention could move in the opposite direction of an eye movement (Berlucchi et al., 1989). Altogether these results indicated that attention and eye movements were either independent processes (Klein, 1980) or separate but functionally related processes (Berlucchi et al., 1980), such that they could be recruited in isolation or in concert depending on task demands. The succeeding "generation" of work has established that attention and eye movements are more tightly related. Shepherd and colleagues (1986) manipulated spatial attention by varying the probability that peripheral probe stimuli would appear in different positions, and eye movements by cueing saccades with a central arrow cue. They found that the preparation of a saccadic eye movement enhanced the manual detection of stimuli presented at the saccadic target location, irrespective of the direction of attention. That is, even when attention and eye movements were cued to opposite locations, stimuli at the location of the saccade were always detected more rapidly. The latency of the saccades was also uninfluenced by the direction of attention. Hoffman and Subramaniam (1995) confirmed in a dual-task situation that target detection is superior at the saccade location regardless of the direction of attention. In this experiment, saccadic latencies were slowest when attention and saccades were directed toward opposite locations. Klein (1980) suggested that processing facilitation at the saccade location is induced by saccadic execution, but not saccadic programming.

The current view is that attention and eye movement systems are tightly related. During the preparation of a saccade, the selection of a location is controlled by the oculomotor system, even when attention is directed elsewhere through cognitive manipulations. This supports an "identity view" in which attention shifts are organized in oculomotor coordinates. Because the direction of attention is dissociable from eye position during fixation, an additional veto-going signal has been postulated to prevent breakdowns of fixation (Rizzolatti et al., 1987). It is still under discussion whether attentional processes are separate when a saccade is planned but not performed, or when the eyes are fixated (Klein, 1994; Rafal et al., 1989). Finally, these findings are consistent with the notion that attention and eye movement systems may be separate but share resources. For example, the slowing of saccadic latencies in Hoffman and Subramaniam (1995) is consistent with some sharing of common resources. However, the prevalent control of saccades on location would suggest that the eye movement system has preferential access to those resources.

1.2 Neuroanatomical models of visuospatial attention: Dorsal vs. Ventral fronto-parietal attentional networks

Several lines of evidence indicate that two cortico-cortical neural systems are involved in attending to environmental stimuli (Corbetta and Shulman, 2002). A dorsal fronto-parietal network, whose core regions include dorsal parietal cortex, particularly intraparietal sulcus (IPS) and superior parietal lobule (SPL), and dorsal frontal cortex along the precentral sulcus, near or at the frontal eye field (FEF), embodies the top-down control mechanism proposed by biased competition and related theories (Bundesen, 1990; Desimone and

Duncan, 1995; Wolfe, 1994). The dorsal system is important in generating and maintaining endogenous signals based on current goals and pre-existing information about likely contingencies and sends out top-down signals that bias the processing of appropriate stimulus features and locations in sensory cortex. This conclusion is based on evidence that the dorsal network is preactivated by the expectation of seeing an object at a particular location or with certain features (e.g., movement in a specific direction) (Corbetta et al., 2000; Hopfinger et al., 2000; Kastner et al., 1999; Shulman et al., 1999), by the preparation of a specific response (Astafiev et al., 2003; Connolly et al., 2002), or by the short-term memory of a visual scene (LaBar et al., 1999; Pessoa et al., 2002). The dorsal system is also involved in linking relevant stimuli to responses, as it is modulated when people change their motor plan for an object (Rushworth et al., 2001). Under some conditions, the preparatory activation of the dorsal fronto-parietal network extends to visual cortex, presumably reflecting the top-down modulation of sensory representations (Giesbrecht et al., 2006; Hopfinger et al., 2000; Kastner et al., 1999; Serences et al., 2004; Silver et al., 2007; Sylvester et al., 2007). Accordingly, anticipatory activity may predict performance to subsequent targets (Giesbrecht et al., 2006; Pessoa and Padmala, 2005; Sapir et al., 2005; Sylvester et al., 2007). Finally, recent studies show that electrical or magnetic stimulation of FEF or IPS leads to a retinotopically specific modulation of visual areas and parallel improvement of perception at corresponding locations of the visual field (Moore and Armstrong, 2003; Ruff et al., 2006, 2007).

To the opposite, the ventral fronto-parietal network is not activated by expectations or task preparation but responds along with the dorsal network when behaviourally relevant objects (or targets) are detected (Corbetta et al., 2000). Both dorsal and ventral networks are also activated during reorienting, with enhanced responses during the detection of targets that appear at unattended locations. For example, enhanced responses are observed when subjects are cued to expect a target at one location but it unexpectedly appears at another (i.e. ‘‘invalid’’ targets in the Posner spatial-cueing paradigm) (Arrington et al., 2000; Corbetta et al., 2000; Kincade et al., 2005; Macaluso et al., 2002; Vossel et al., 2006) or when a target appears infrequently.

Core regions of the ventral network include temporoparietal junction (TPJ) cortex (anatomically defined as the cortex at the intersection of the posterior end of the STS, the inferior parietal lobule, and the lateral occipital cortex), defined as the posterior sector of the superior temporal sulcus (STS) and gyrus (STG) and the ventral part of the supramarginal gyrus (SMG) and ventral frontal cortex (VFC), including parts of middle frontal gyrus (MFG), inferior frontal gyrus (IFG), frontal operculum and anterior Insula.

An early theory of how the two networks interact (Corbetta and Shulman, 2002) proposed that when attention is reoriented to a new source of information (stimulus-driven reorienting), output from the ventral network interrupts (as a ‘‘circuit breaker’’) ongoing selection in the dorsal network, which in turn shifts attention toward the novel object of interest. Although both attentional networks have been most extensively investigated in vision, the available evidence indicates a supramodal function (Driver and Spence, 1998;

Macaluso et al., 2002). The ventral network (TPJ and IFG in the right hemisphere) registers salient events in the environment also in the auditory and tactile modalities (Downar et al., 2000), and similar dorsal and ventral parietal and frontal regions are modulated by reorienting to invalid targets (Arrington et al., 2000; Corbetta et al., 2000; Giessing et al., 2006; Kincade et al., 2005; Macaluso et al., 2002; Mayer et al., 2006; Vossel et al., 2006).

The Dorsal and Ventral Attention Systems form separate functional-anatomical networks and a basic question is the degree to which different regions in each putative system cohere as a functional-anatomical network. The hypothesis of two attention networks, originally based on the patterns of activation under different task conditions (Corbetta and Shulman, 2002), has been strongly supported by studies of interareal correlation of low-frequency (<0.1 Hz) fluctuations of the spontaneous (not task-evoked) BOLD signal over time, called functional connectivity by MRI (fcMRI) (Biswal et al., 1995). Several groups have reported a number of fcMRI networks (e.g., visual, auditory, somatomotor, default, attention) (Fox et al., 2005b, 2006a; Fransson, 2005; Greicius et al., 2003; Mantini et al., 2007), which are related to the underlying anatomical connectivity (Vincent et al., 2007) and replay at rest the patterns of functional activation evoked by behavioral tasks (Fox et al., 2005b, 2006a; Greicius et al., 2003; Hampson et al., 2002; Vincent et al., 2007). In other words, brain regions that are commonly recruited during a task are anatomically connected and maintain in the resting state (in the absence of any stimulation) a significant degree of temporal coherence in their spontaneous activity. Furthermore, there is growing evidence that the integrity and strength of spontaneous functional connectivity are behaviorally significant (Hampson et al., 2006; Seeley et al., 2007; He et al., 2007b). For instance, breakdown of interhemispheric functional connectivity in posterior parietal cortex correlates in a group of patients with post-stroke neglect with their visuospatial deficits (He et al., 2007a). Regions that putatively belong to the dorsal and ventral attention systems, based on their consistent activation in the Posner cueing paradigm to spatial cues and unattended targets, respectively, also show significant interregional correlation at rest (Fox et al., 2006b) or during an active task with the mean task signal removed (He et al., 2007a). There is a remarkable similarity between the dorsal parietal and frontal regions identified by a meta-analysis of task-evoked activation studies and those showing high resting-state correlations. Similar results are found for ventral frontoparietal regions coactivated during stimulus-driven orienting (Fox et al., 2006a; He et al., 2007a). Moreover, the right hemispheric bias observed in the ventral attention network in several activation studies (Arrington et al., 2000; Corbetta et al., 2000; Downar et al., 2000) is mirrored in fMRI (Fox et al., 2006a; He et al., 2007a). While segregation between dorsal and ventral attention networks is nearly complete, spontaneous activity in right posterior MFG correlates with both networks, indicating that right MFG may contain intermixed neuronal populations respectively connected with dorsal or ventral regions (Fox et al., 2006a). This result raises the possibility that ventral and dorsal networks do not directly interact but are principally linked through prefrontal cortex (Fox et al., 2006a). The functional segregation of the two networks in the absence of a task may allow their flexible recruitment during active behavior. For example, while dorsal regions are active following the presentation of an instructive cue, ventral regions are not recruited or are even suppressed (Shulman et al., 2003; Todd et al., 2005). However, following the presentation of a target, both ventral and dorsal regions respond briskly (Corbetta et al., 2000; Hampshire et al., 2007; Shulman et al., 1999, 2003).

To conclude, the correspondence between activation and connectivity analyses provides strong evidence for separate dorsal and ventral attention networks forming distinct functional systems. The Ventral Network is activated by important stimuli that reorient attention. While reorienting to an object can be driven by salience and behavioral relevance, relevance is the critical factor that determines whether an object activates the ventral network (Downar et al., 2001). Thus, the ventral network might be considered a prime candidate for mediating orienting to salient but unimportant stimuli, i.e., exogenous attention (Posner and Cohen, 1984), because under passive conditions it is highly responsive to distinctive sensory events in all modalities (Downar et al., 2000). But this hypothesis has now been tested and rejected (Kincade et al., 2005). Kincade and colleagues separated the BOLD activity produced by an uninformative but salient peripheral cue, a red square in an array of green squares, from the activity produced by discriminating a subsequent rotated T or L. In control conditions, subjects were presented with a neutral display of randomly intermixed color squares or a foveal cue that oriented attention voluntarily. Exogenous cues (the red square) did not activate the ventral network , even though performance was better at that location, indicating that these cues were effective in generating a shift of attention. In contrast, the dorsal network (IPS/SPL and FEF) showed stronger activation for exogenous than neutral cues, although the strongest recruitment was recorded for endogenous cues (data not shown). Many other studies have measured activations in exogenous orienting paradigms that have combined activations during the cue and target periods (Kim et al., 1999; Lepsien and Pollmann, 2002; Mayer et al., 2006; Peelen et al., 2004; Rosen et al., 1999). Although these studies are more difficult to interpret, they indicate that the ventral network is not recruited by orienting to uninformative but salient cues presented before a target appears (see Peelen et al., 2004, for an exception). Similarly, de Fockert and colleagues (2004) showed that uninformative but salient distracters that attract attention did not activate the ventral system, although they did activate the dorsal system.

The overall conclusion is that exogenous orienting recruits the same dorsal fronto-parietal network that is responsible for directing attention based on goals or expectations. Conversely, the ventral network is well activated by stimuli that are important, even if they are not very distinctive. Indovina and Macaluso (2007), for example, showed that unattended targets of low salience activated regions in both dorsal (FEF, precuneus) and ventral (IFG and anterior insula) attention networks, in line with previous results (Arrington et al., 2000; Corbetta et al., 2000; Macaluso et al., 2002), to a much greater degree than highly salient but irrelevant distracters. Finally, the ventral network is activated by irrelevant objects when they are similar to a target object. Serences et al. (2005) asked subjects to categorize red foveal letters interspersed among a rapid, successive series of colored foveal letters (rapid serial visual presentation, or RSVP) while peripheral distracter letters were occasionally presented in the target color (red) or in a non-target color (green). This situation is analogous to when we look in a crowd for a friend wearing a red sweater and notice people wearing red but not green clothes (‘‘contingent’’ orienting; Folk et al., 1992). TPJ activation was only observed for the red distracters, consistent with the hypothesis that the ventral network responds mainly to stimuli thought to be behaviorally relevant (see also Downar et al., 2001). In summary, the ventral network is not activated by orienting to distinctive but unimportant stimuli (exogenous orienting), except perhaps in the special case where subjects do not have an ongoing task, but does underlie reorienting to environmental stimuli based on their task relevance. An important conclusion from these neuroimaging studies is that the psychological distinction between exogenous and endogenous orienting (Jonides, 1981) may not map onto different neural systems. Rather, a more fundamental distinction appears to be between systems involved in orienting, both exogenous and goal-driven, i.e., the dorsal attention system, and those involved in stimulus-driven reorienting, i.e., the ventral and dorsal attention systems.

Chapter 2

Reflexive orienting to Biological vs. Non-Biological cues: Gaze, Pointing and Arrow

A fundamental aspect of attentional shifts resides in their directionality. As mentioned in Chapter 1, orienting of attention may be either entirely voluntary or triggered by external stimuli presented in the peripheral or in the central part of the visual field. It has been held that attention was automatically and reflexively triggered by peripheral stimuli and not by central stimuli (Posner et al., 1980). However, it is now known that even central stimuli can reflexively catch attention particularly when these stimuli have high social valence such as for example directional gaze stimuli (Driver et al., 1999; Friesen and Kingstone, 1998). Indeed, the behaviour of individuals belonging to highly social groups (e.g. human and non-human primates) is profoundly influenced by others' gaze. Detecting others' gaze direction provides helpful cues on their overt behaviour (e.g. deriving information about a potential danger from the gaze of the observed subject) as well as on their mental states (emotional, intentional) (Emery, 2000). Thanks to these mechanisms we can implement a series of predictive behaviours that are crucial to individual and social adjustments. Gaze direction is fundamental for the interindividual sharing of attention as attested by the fact that two-month babies spend more time in looking at the eyes than at other face regions (Maurer, 1985; Batki et al., 2000; Farroni et al., 2002) and smile to ocular contacts (Aitken and Trevarthen, 1997). Moreover, four-month babies perceive others' gaze and interpret it as directional cue (Farroni et al., 2000).

Another important biological cue that proved to influence the shifts of social attention is the directional indication provided by a pointing hand (Butterworth et al., 1998; O'Neill, 1996). Through pointing humans are able, already at 14 month of age, to catch visual attention of another individual and to re-direct it towards specific objects or spatial locations (Butterworth, 1998). In humans, producing and understanding pointing gestures is a fundamental pre-requisite for social interactions in that these cognitive operations allow the interindividual communication and provide the ability to link words to objects (Horne and Lowe, 1996). In particular, the "protodeclarative" pointing signals to other individuals potentially interesting objects and places.

In the next sections, I will review some critical points about social valence and neural bases of normal gaze perception. In the same vein, I will introduce some basic concepts of social meaning and neural underpinning underlying the processing of pointing hand gesture.

2.1 Gaze perception, Theory of Mind (ToM) and Joint attention mechanisms

The direction of someone else's gaze typically signifies where his/her attention is being directed. The term "joint attention" refers to a triadic relationship involving two persons (A and B) and one object, as both person attend to the same object. In other words, when the gaze direction of B will inform A of his attention onto the object and A will also attend to it, this is called "*Joint Attention*". However, only one of them uses the other's gaze direction to orient to the same target (A sees that B looks at the object and A then looks at the object). When both individuals are aware of each other's object of attention and a check that both individuals attend to the same target is do, than the proper definition is *"Shared Attention"*. This implies that A sees that B looks at the object and will attend to the object; B notices that A attends to the object too and A and B look at each other's eyes (mutual gaze) to make sure they both attend to the same object. This mechanism of Shared attention is more complex than joint attention and both play fundamental roles in social cognition (See Figure 1).

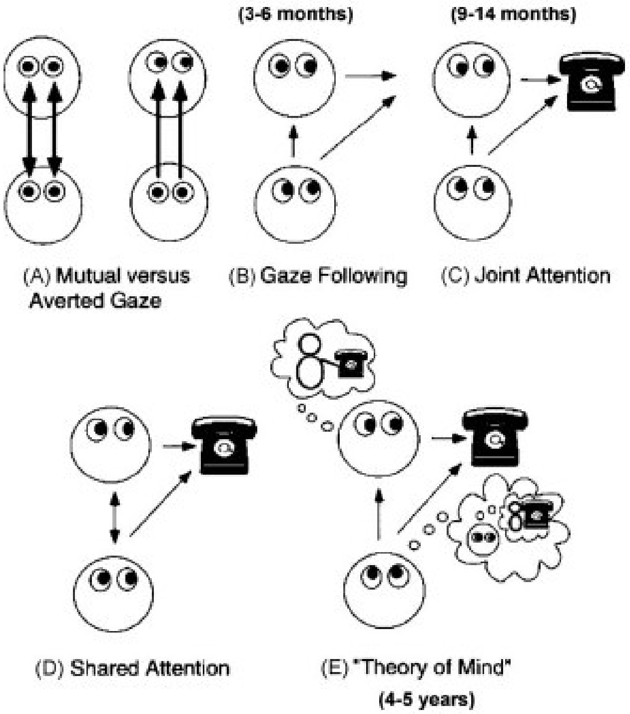


Figure 1. Schematic depiction of the various social situations involving the use of gaze direction. The ages at which the various capabilities emerge are in parenthesis. (Adapted from Emery, 2000).

Gaze following has been reported as early as 3–6 months of age (D'Entremont et al., 1997), although the exact age at which this capacity emerges is controversial (Emery, 2000). Before 9 months, infants can follow their mother's gaze but are not capable of directing their attention towards the object of her interest. The joint attention capacity, which includes not only gaze monitoring but also pointing gestures, emerges around 9–14 months (Baron-Cohen et al., 1997a) but it's only around 18 months of age that infants can attend to the same object of interest as their mother if the object is situated outside of their own visual field such as behind them (Butterworth, 1991).

Joint attention is fundamental for the acquisition of language, because initiate the association between a word and the object it represents. Being able to orient one's attention in the direction of gaze of the person naming the object is thus crucial (Baldwin, 1993; Baron-Cohen et al., 1997a). For example, if a mother says ‘‘cat’’ while looking at a cat, a child listening for the first time to this word will orient his attention in the gaze direction of the mother and will associate the word to its meaning. This learning strategy based on the use of people's gaze direction emerges between 12 and 19 months of age (Baron-Cohen et al., 1997a) and positive correlations between gaze-following at 10–11 months of age and subsequent vocabulary scores at 18 months have been shown (Brooks and Meltzoff, 2005). A recent modelling study showed that gaze-following behavior at 10–11 months of age significantly predicted accelerated vocabulary growth until 2 years of age, even after controlling for the effects of age and maternal education (Brooks and Meltzoff, 2008).

Baron-Cohen (1995) proposed the existence of an innate module specialized in the detection of gaze direction (eye direction detector, EDD), because of the important role of gaze early in development. Firstly, EDD would detect any eyelike stimulus than it would determine whether the observed gaze is directed towards oneself or elsewhere. This module would play an essential role in the development of shared attention and in Theory of Mind (ToM). The term ToM refers to the capacity to explain others' behaviors in terms of mental states, such as intentions, desires and beliefs and was originally introduced by primatologists to describe the possibility that chimpanzees understood certain mental states in other chimpanzees (Premack and Woodruff, 1978). This capacity was called a "Theory of Mind" because it is impossible to directly access others' minds; we are simply guessing and inferring their mental states. ToM skills emerge around 4–5 years of age (Mitchell and Lacohée, 1991) and usually is assessed by using cartoon tests portraying social situations in which understanding false belief is essential (Wimmer and Perner, 1983; Brune and Brune-Cohrs, 2006). In addition, a module called the intentionality detector (ID) has also been proposed. The ID understands any movement in the environment in terms of volitional movement, i.e. the goal-directed movement of an external agent (Baron-Cohen, 1995). Both EDD and ID would contribute to the development of shared attention, itself necessary for the development of ToM. Finally, Perrett and Emery (1994) proposed a direction-of attention-detector (DAD) module that could process not only gaze cues but any attentional cue including head and body orientation. They also proposed a mutual attention mechanism, suggesting the activation of EDD or DAD would be necessary for joint attention while shared attention would require the activation of the mutual attention mechanism in addition to EDD or DAD.

In Baron-Cohen's Theory, gaze direction is thus an important and privileged stimulus for the attribution of mental states. A test based on photographs of isolated eye regions has even been developed for the evaluation of ToM capacities in adults (Baron-Cohen et al., 1997b, 2001a) and in children (Baron-Cohen et al., 2001b). In this force-choice test, subjects need to designate, amongst four words evoking a mental state (e.g. preoccupied, puzzled, reassuring, jealous), which one best describes the eye region presented. This test was called the "reading the mind in the eyes" test and was found appropriate in revealing ToM impairments in special clinical populations such as autistic spectrum disorders. The processing of gaze is thus an extremely important step in developing a social cognition and a theory of mind and relies on a very rich neural network.

2.1.1 Brain areas involved in gaze processing

Numerous PET and fMRI studies have shown that gaze processing, usually studied with faces rather than isolated-eye stimuli, involves mainly the superior temporal sulcus (STS) region (Allison et al., 2000; Bristow et al., 2007; Hoffman and Haxby, 2000; Hooker et al., 2003; Pelphrey et al., 2003; Puce et al., 1998; Wicker et al., 2003). The role of STS relies to the processing of biological motion, with gaze being a specific type of biological motion (See Puce and Perrett, 2003). The STS is also involved in the gaze orienting effect but not in attention-orienting to arrows (Kingstone et al., 2004). However, discrepancies are found in the comparison between averted and direct gaze conditions. Some studies have found larger activations of the STS for direct gaze (Calder et al., 2002; Pelphrey et al., 2004; Wicker et al., 2003) while others have found larger activation of that region for averted gaze (for the left STS, Hoffman and Haxby, 2000). Moreover, some other studies have not found STS differences between averted and direct gaze (Pageler et al., 2003). To the opposite, a study of Hardee and colleagues (2008) reported the non-selectivity of the STS for gaze direction or emotion from eye regions in agreement with recent monkey data (Hoffman et al., 2007). In other gaze processing studies however, the STS is not even activated (George et al., 2001). It has to be emphasized that the term STS region is general and some studies report anterior areas (e.g. Calder et al., 2007; Kingstone et al., 2004) while others report posterior ones (sometimes referred to as pSTS, See Allison et al., 2000). Therefore, the no-convergence of results could be due to a difference in the actual localization of the so-called STS region in addition to differences in the paradigms and stimuli used.

Another key brain structure involved in processing the eyes and their gaze is the Amygdala. Although conflicting results were found about the role of this region, it has been proposed that the amygdala responds to gaze and to emotion underlying specific and devoted neural nodes. For example a fMRI study of Adams and colleagues (2003) who used only front-view faces, found that the left amygdala responded more to an angry face with averted rather than direct gaze and more to a fearful face with direct rather than averted gaze. The conclusion was that Amygdala reflects the ambiguous source of threat expressed by these faces. In another study, in which head orientation always matched gaze direction so that the averted gaze condition was in fact a 3/4-view face with averted gaze, the authors found the opposite results, with larger left amygdala response to direct than averted-gaze angry faces (Sato et al., 2004). Interestingly, Sato et al.'s study showed a positive correlation between the activation of the left amygdala and the negative emotion experienced by the subjects in viewing these faces, but not with the perceived negative emotion of the faces which did not differ between the two gaze/face orientations. The authors suggested that the amygdala activation reflects the emotional significance of the facial expression and the viewer's emotional reaction towards the expression (Sato et al., 2004). A recent study also suggests a hemispheric difference in amygdala response linked to the type of eye stimulus used. The left amygdala activated only for fearful eyes but not for gaze shifts even though the eye white area had been equated between gaze and fear conditions, while the right amygdala responded to all conditions equally, including joyful and control eyes (Hardee et al., 2008). These results contrast with the idea that the amygdala responds only to the eyes' white area (Whalen et al., 2004) and rather suggest a hemispheric difference in stimulus selectivity for this structure. According to Hardee et al. (2008) hypothesis the lack of selectivity of the right amygdala could reflect a mechanism tuned to the fast and coarse detection of potential dangers, while the left amygdala could reflect a mechanism tuned to details enabling the verification of whether the threat is real. Thus, in addition to its likely role in orienting attention towards the eye region, results from the neuroimaging literature suggests the amygdala response may not be modulated by gaze direction per se but rather by the emotional implication of a given stimulus for the subject in a particular task context. This interpretation may explain why, like the STS region, discrepancies between direct and averted gaze have been found for the amygdala. In addition to the stimuli and possible personal emotional involvement of subjects, these inconsistent results (including for the STS and amygdala) could be due to a different sensitivity of all these areas to a specific gaze direction depending on the subject's task.

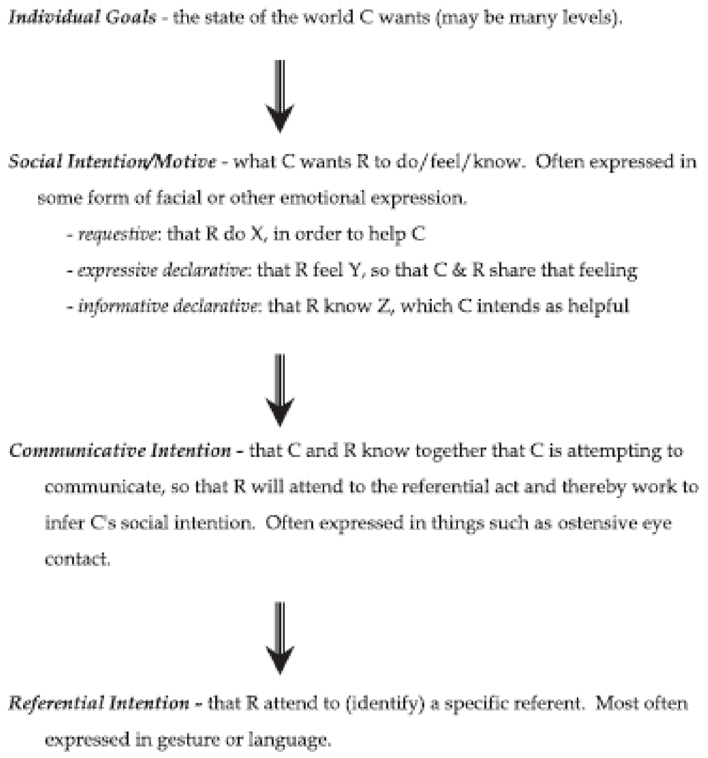
In agreement with the recent neuropsychological study (Vecera and Rizzo, 2006), a few neuroimaging studies also reported the involvement of frontal areas during gaze processing. For example, a recent study (Calder et al., 2002) in which direction of gaze was manipulated implicitly while subjects had to judge the size of the eyebrows of face pictures, reported activation of frontal regions. In addition to the STS region, a larger activation was found in medial frontal areas (BA8/9 and BA10) for averted compared to direct gaze or even faces with closed eyes. This bilateral activation of superior frontal regions (BA8) was also reported in an explicit gaze direction judgment (Hooker et al., 2003). The involvement of the superior and medial frontal gyri (BA6) was reported in another gaze study (Wicker et al., 1998) but as the task was passive, it is difficult to know whether this region was involved in gaze processing per se or was responding to other factors. Similarly, the isolated eyes of Hardee et al. (2008) involved bilateral activation of the orbitofrontal cortex (OFC) that was not selective to gaze shift or emotion but it is difficult to interpret the involvement of this region as the task was implicit. Importantly, these frontal regions, especially the medial prefrontal and orbitofrontal cortices, are found in numerous ToM and joint attention studies, just like the STS and the amygdala (Adolphs, 1999; Amodio and Frith, 2006; Williams et al., 2005). This suggests that gaze processing recruits a large network of brain areas involved in ToM and social cognition and that the various degrees of involvement of each of these regions depends on the specific task utilized.

Finally, a few studies have also reported the activation of some parietal areas in gaze perception. The intraparietal sulcus (IPS) was reported for the viewing of averted eye movements (Bristow et al., 2007; Hardee et al., 2008; Pelphrey et al., 2003) and perception of averted gaze in static faces (Hoffman and Haxby, 2000). Other studies have reported the activation of the inferior parietal and superior parietal lobules for the movement of eyes within faces (Calder et al., 2007; Wicker et al., 1998). Most important, because the parietal cortex including the IPS is involved in covert shift of spatial attention (Corbetta and Shulman, 2002; Grosbras et al., 2005), gaze-related activity in these regions is usually thought to reflect the engagement of the attentional system for encoding the spatial direction of another's gaze and orienting attention in that direction. This general role is supported by the non-selectivity of that region for gaze as reported by Hardee et al. (2008). Although, the review of the neuroimaging literature on gaze perception confirms the results from the neuropsychological literature regarding the involvement of the amygdala, the STG/STS, the FG, some parietal and frontal areas, in agreement with a fronto-parietal circuit for gaze as found in a meta-analysis involving 59 neuroimaging studies (Grosbras et al., 2005), this analysis also found that gaze perception shared common neural substrates with visually triggered saccades and visually triggered shifts of attention (Grosbras et al., 2005). In particular, the temporo-parietal junction (TPJ) area, which is adjacent to the pSTS region is common node both shared by gaze direction perception and visually triggered saccades. However, the precise role of these regions in processing direct or averted gaze and the influences of task demands remain to be better understood.

2.2 Pointing with the index finger

An especially important gesture that has a number of unique features is human pointing. Although there may be some variations of form, pointing is characterized by a basic interpersonal function of directing someone's attention to something is very likely a human universal (Kita, 2003). Pointing is a special gesture that can convey an almost infinite variety of meanings such as: ''If you look over there, you'll know what I mean.'' To recover the intended meaning of a pointing gesture, therefore, requires some fairly serious ''mindreading.'' Infants begin to point to things for other persons from around 11 to 12 months of age (Carpenter, Nagell, and Tomasello, 1998; Leung and Rheingold, 1981). Bates, Camaioni, and Volterra (1975) conceptualized it as a kind of social tool use, as infants begin to use physical tools at around this same age. According to "Speech Act Theory", it is possible to distinguish between two types of communicative act that have formed the basis for all subsequent accounts of pre-linguistic communication. The first is “protoimperative” pointing and an infant points to get the adult to retrieve an object for them: “He/she uses the adult as a tool to obtain the object”. Instead, “protodeclarative” pointing implies that infant points to get the adult to attend to an external entity: “He/she uses the external entity as a tool to obtain adult attention”. The current theoretical debates about infant pointing raise the question whether young infants are attempting in their pre-linguistic communication to influence the intentional/mental states of others (cause them to ‘‘know’’ something) or whether, alternatively, they are simply aiming to achieve certain behavioral effects in others (cause them to ‘‘do’’ something). For example, Camaioni (1993) proposes that protoimperative gestures emerge first in development and only require the infant to understand the other as a causal agent not a mental agent who makes things happen behaviourally, whereas protodeclarative gestures emerge later and require the infant to understand the other as a mental agent whose attention may be directed to external entities. Moore and colleagues (1996) claimed that even protodeclarative gestures initially, at least are not directed at the intentional/mental states of others, but are simply directed at gaining adult attention to the self. Pointing simply directs someone’s attention to a location in the perceptual environment, but to correctly identify the intended referent requires that the communicator and the recipient know together that the indicated location is in some way relevant to some larger context they share. We will call this larger context, following Clark (1996), common ground or the “joint attentional frame”. And it must be emphasized that the common ground or joint attentional frame within which pointing gains its meaning is, of necessity, common or joint. It is important that common ground need not be personal in the sense that you and I have personally experienced things together. In addition to knowing exactly what in their common ground a pointer is referring to, recipients must also determine why the communicator is pointing.

The most important question about pointing social meaning is that we have to distinguish at least two levels of intentionality involved in every communicative act: the communicator's more narrow referential intention of directing the recipient's attention to something, and his wider social intention or motive for directing her attention there in the first place, in the sense of what he wants her to know or to do. Human motivations for communicating are mainly cooperative. Thus, the three most basic motivations may be characterized in terms of helping and sharing (the other two are also cooperative in different ways): 1) informative (assertive): the communicator wants the recipient to know something that he thinks she will find useful or interesting he is helping her by informing her; 2) requestive (directive): the communicator wants the recipient to do something that will help him, the communicator, in some way (including by providing needed information, as in questions); and 3) expressive: the communicator wants the recipient to feel some attitude or emotion that he is already feeling he wants her to share this attitude or emotion with him. To help you to infer my social intention, I will often produce some kind of overt (emotional) expression. Also of interest here is the mutual assumption of helpfulness both communicators trust that the other will make good faith attempts to collaborate in getting the communicator's message across (Clark, 1996) which underlies and indeed makes possible the kind of cooperative communication characteristic of the human species. Inferring the communicator's social intention (her motive, why he/she is pointing for me) also depends crucially on the common ground between communicator and recipient. To summarize, Figure 2 depicts the different layers of intentionality underlying a communicator's pointing act in the current analysis. Beyond any individual goals, we must recognize: the social intention (that you do/know/feel something); the communicative intention (that we know together that I want one of these things from you); and the referential intention (that you attend to something as a way of figuring out what it is I want from you).



Individual Goals - the state of the world C wants (may be many levels).

Social Intention/Motive - what C wants R to do/feel/know. Often expressed in some form of facial or other emotional expression.

- *requestive*: that R do X, in order to help C
- *expressive declarative*: that R feel Y, so that C & R share that feeling
- *informative declarative*: that R know Z, which C intends as helpful

Communicative Intention - that C and R know together that C is attempting to communicate, so that R will attend to the referential act and thereby work to infer C's social intention. Often expressed in things such as ostensive eye contact.

Referential Intention - that R attend to (identify) a specific referent. Most often expressed in gesture or language.

Figure 2: Different levels of goals/intentions underlying pointing as a human communicative act, from the communicator's perspective (C: communicator; R: recipient). Arrows indicate that the higher goal/intention is carried out by means of the lower one. (Adapted from Tomasello, Carpenter and Liszkowski, 2007)

2.2.1 Brain areas involved in pointing gesture

In addition to gaze and arrow cues, current social neuroscience literature suggests that hand-pointing gesture may automatically trigger attentional shift. An experimental study in adults showed that hand-pointing gestures were processed automatically (Langton and Bruce, 2000). The researchers used the interference effect of stimulus presentation on the processing of spoken directional words. Their results confirmed that hand-pointing presentation produced an automatic interference effect. These data suggest that hand pointing may trigger attentional shift in the same automatic manner as the eyes apparently do, although to date no studies tested this issue.

To our knowledge only a recent study published by Sato and collaborators (2009) investigated the commonalities in the neural mechanisms underlying automatic attentional shifts by gaze, hand gestures, and symbolic arrow. The authors measured the brain activity using fMRI while participants observed directional and non-directional stimuli, including eyes, hands, and arrows. Conjunction analyses revealed that the posterior STS, the IPL, the IFG, and the occipital cortices in the right hemisphere were more active in common in response to directional versus non-directional stimuli (see Figure 3).

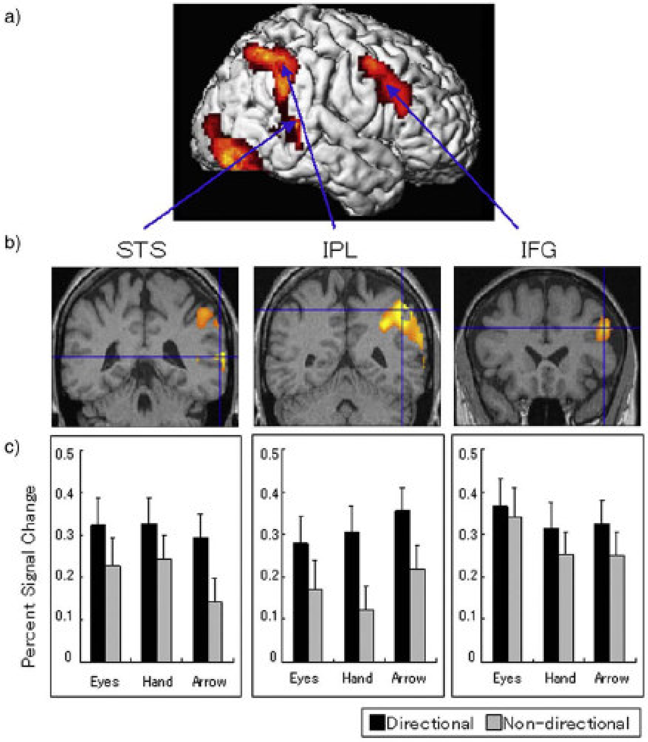


Figure 3: **(a) Statistical parametric maps indicating the brain regions that were activated in common in response to directional versus non-directional stimuli depicting eyes, hands, and arrows. (b) Statistical parametric maps of the representative brain regions that exhibited higher activation for directional versus non-directional stimuli depicting eyes, hands, and arrows.** STS=superior temporal sulcus region; IPL=inferior parietal lobule; IFG=inferior frontal gyrus. (c) Mean percent signal changes (with SE) of representative brain regions that were highly activated in response to directional versus non-directional stimuli depicting eyes, hands, and arrows. (Adapted by Sato et al., 2009)

These results suggest commonalities in the neurocognitive mechanisms underlying the automatic attentional shifts triggered by gaze, gestures, and symbols. Consistently with previous studies (e.g., Hietanen, 1999; Hommel et al., 2001), the data support the hypothesis that eyes, hands, and arrows could automatically trigger a similar pattern of attentional shift. These common psychological mechanism involved in the automatic attentional shift by gaze, gestures and symbols are consistent with human developmental studies that indicate that infants follow the direction of attention of adults, which were indicated by eyes or hand-pointing gestures (Csibra, 2003). An animal study also indicated that chimpanzees showed automatic attentional shifting while viewing arrows (Itakura, 2001). These developmental and comparative data suggest that a shared psychological mechanism in human beings for the automatic attentional shift in response to gaze, gestures and some kinds of symbols may have developed through the evolutionary process. Nevertheless, one methodological limitation of this study should be noted. Because the authors did not use a cueing paradigm during image scanning, the direct link between neural activity and behavioral performance remained untested. Future research that examines the relationship between brain activity and behavioral performance may provide further evidence regarding the brain mechanisms involved in the cognitive functions subserved by the brain activity we observed.

Therefore, the main objective of our first fMRI study was to overcome this limitation by exploring the interaction between the category of task-irrelevant visual stimuli (eyes, hands, or non-biological cues, i.e. arrows) and the motor-effector (eyes vs. hands) during the orienting task (See Chapter 5).

Chapter 3

*Towards a "S*ocial Somatotopy*" of*
Reflexive Social Attention

The brain contains multiple representations of the body. First, afferent inputs from the skin and proprioceptive receptors project to maps of the body surface and body segments in the primary somatosensory cortex (Penfield and Rasmussen, 1950). These somatotopic maps reflect the distribution of sensory receptors within the body, and underpin somatic sensation (Romo et al., 1998). For example, area 3b contains a distorted "homunculus", with enlarged lips and hands. Neuroanatomical, neuropsychological and neurophysiological evidence all suggest that this primary information is further processed to construct higher-order, more cognitive representations of the body. These representations differ from primary maps in providing a supramodal, coherent scheme for body representation and skilled action.

3.1 Body representations: body schema and body image

At the cognitive level, a fundamental distinction can be made between two different higher-order body representations which have been called *body schema* and *body image* (Paillard, 1999). *Body schema* refers to a representation of the positions of body parts in space, which is updated during body movement. This typically does not enter into awareness and is primarily used for spatial organization of action. The body schema is therefore a central representation of the body's spatial properties, that includes the length of limb segments, their hierarchical arrangement, the configuration of the segments in space and the shape of the body surface. *Body image* refers to a conscious visual representation of the way the body appears from the outside, typically in a canonical position. The scientific concept corresponds roughly to the everyday use of the term. Moreover, the term schema has other uses in cognitive science. Haggard and Wolpert (2005) refer to body schema as "a neural representation of the body used for spatial sensorimotor processing, by excluding representations for primary sensory input and motor execution".

The body scheme could be characterized by the following seven fundamental properties of body representation:

1. **Spatially coded:** the body scheme represents the position and configuration of the body as a volumetric object in space. Crucially, the body scheme integrates tactile information from the body surface with proprioceptive information about the configuration of the limbs in

space (Head and Holmes, 1911). This integration means that a stimulus on the body can be localized in external space.

2. **Modularity:** body postures might be stored as individual entries in a database by describing the entire body configuration and body surface stimuli. However, the evidence suggests that the brain represents different body parts in different neural modules, using the resulting modular network to represent all postures. Therefore, the body scheme comprises body parts or segments, which bear spatial and categorical relations to each other (e.g., fingers are elements of hands, which form the ends of arms) (Tessari and Rumiati, 2002).
3. **Updated with movement**: any body representation we used during an action must continuously track the positions of our body parts as we move. The updating process may underlie the finding that the visual receptive fields of many parietal neurons follow the hand when the hand moves (Graziano and Gross, 1993). This mechanism would allow the body scheme to modulate perceptual processing of objects according to their position in peripersonal space. This would be essential for control of grasping or avoidance movement.
4. **Adaptability**: the body scheme is able to adapt in order to obtain gradual changes in the spatial properties of the body. In addition the body scheme can change on a shorter time scale to incorporate additional objects as new segments of the body representation. These plastic changes may occur both as gradual extensions to an existing

scheme, or as rapid switches between several alternative coexisting schemes (Braun et al., 2001).

5. **Supramodality**: because the body scheme receives multiple sensory input, it is able to integrate body surface information and proprioception to describe the body as a volumetric object in external space. In addition, however, visual information can be in the same representation. Thus, a visual stimulus and a tactile stimulus at the same location on the body surface may form a joint representation within the body scheme (Rorden et al., 1999). This may involve transforming primary representations of vision, proprioception and touch either into a single sensory modality, or into an abstract, amodal code.
6. **Coherence**: the brain must be able to maintain a coherent spatial organization of the body scheme across space and time, in order to ensure a continuity of body experience which may play a major role in individual self-consciousness. A basic principle of body scheme coherence is the resolution of inter-sensory discrepancies. For example, the visual and proprioceptive representations of hand position each have characteristic biases and variabilities, yet we perceive our hand in a single location because the brain optimally combines these sources of information (van Beers, Wolpert, and Haggard, 2002). These discrepancies can be exaggerated by experimental manipulations which put the modalities into stark conflict. For example if the forearm is held at a fixed extension angle and the biceps tendon vibrated an

illusory extension of the forearm is experienced. If a blindfolded subject holds his nose during this procedure, the nose is perceived to grow in length as the forearm is felt to extend. In this case, the proprioceptive information from the arm, and the tactile information about the contact between the fingers and nose are preserved and made coherent by adapting the perceived size of another body part (the nose). The overall coherence of the body scheme is thus preserved by altering the representation of a single body segment.

7. **Interpersonality:** a common body scheme is used to represent both one's own body, and the bodies of others. Reed and Farah (1995), for example, showed that participants could better perceive changes in a model's body posture if they simultaneously moved their own corresponding body part. These results imply that the observed and self-generated actions were co-represented within a single modular body scheme. An interpersonal function necessarily implies a supramodal body scheme, since information about others' bodies is generally visual, while information from one's own body is generally tactile or proprioceptive.

Several lines of evidence show that a common neural body scheme is used "*interpersonally*" to represent both one's own body and others' bodies. This implies a mapping function linking the codes for specific body parts across people. Therefore, a surprising but fascinating feature of the brain's body scheme is the "commonality" between the representation of one's own body and the body of other individuals. This suggests that the body scheme could also form a basis for social cognition.

3.2 Body-part specific reference frames for mapping reflexive joint attention

A study published by Ricciardelli and colleagues (2002) demonstrated that healthy subjects tend to imitate the oculomotor behaviour of other individuals reflexively. Importantly, they found that the distracting effect of others' gaze directed left- or rightward is significantly higher than the distracting effect of leftward or rightward pointing arrows and the interferential effect was maximal when the distracter preceded the instruction signal. The authors linked the results to "a tendency to share a common attentional state of another person", seen that this effect was specific for body-part as the observed gaze and not for directional no-biological signal as arrows.

By using a similar joint attention paradigm, Crostella et al (2009) non only replicated (only for saccadic task) but also demonstrated that gaze and pointing hand distracters that were directionally incongruent with the instruction-cue respectively impaired the goal-driven saccadic and pointing performance thus suggesting that reflexive social attention is mapped in a "somatocentred" fashion and not only in a spatial reference frames. By comparing the attention-catching power of directional gaze, hand and arrow cues presented before, simultaneously or after an instruction cue signalling actions to be performed with eyes or hand, the authors found a specific relationship only between reflexive joint attention and distracting stimuli with social/biological valence, (i.e. gaze and hand). This is in keeping with studies showing that when one person observes another suddenly shifting gaze or pointing, the observer's attention automatically and rapidly orients to the same location even when orienting is not relevant or is even detrimental to the task (Driver et al., 1999; Friesen et al., 2005; Langton et al., 1996; 2000).

The novelty of the study concerned two main core issues. The first was that the interference effect of social stimuli occurred “only” when the distracting stimulus preceded the instruction to move. This indicates that the detrimental effect is due to interference with ongoing action programs in accord with “Premotor Theories of Attention” (Rizzolatti et al, 1987). Second, it has been proposed that the social modulation of reflexive attention does not reflect purely spatial codes but is also mapped according to “somatocentred” rules. To better clarify the concept, I would stress the results of this study by remarking that while the distracting gaze impaired saccadic performance significantly more than distracting biological-social (hand) or non biological stimuli (arrows), the distracting hand impaired pointing performance significantly more than distracting gaze or arrows. On the basis of these results, the authors concluded that the higher interference of social cues does not occur according to mere coding of a given position in space but it is influenced by the relation between the body part depicted in the distracter and the body part which performs the action requested by the experimental task.

Studies of visuospatial attentional shifts have linked pointing and saccadic responses to exogenous and endogenous cuing respectively. The phenomena reported in the Crostella’s study are reminiscent of behavioural studies that show a facilitation of hand grasping performance during observation of a hand in a congruent but not in an incongruent position (Craighero et al., 2002). In a similar vein observing another person making incongruent movements has a significant interference effect on movement execution that was not found during observation of a robotic arm making incongruent movements (Kilner et al., 2003). The close link between specific visual stimuli and specific motor actions is also suggested by neurophysiological studies on the motor mirroring of observed hand actions (Fadiga et al, 1995; Romani et al, 2005; Urgesi et al, 2006). The notion that a similar mirror system may exist also for the oculomotor domain is supported by the finding that similar, mainly fronto-parietal and temporal, cortical regions are recruited during execution and observation of eye movements (Grosbras et al., 2005). To conclude, these studies significantly extended previous knowledge by showing that reflexive shifts or visuospatial attention are modulated by social body stimuli through a “sensorimotor mirroring process” that takes place according to body-part specific reference frames.

3.3 Fronto-parietal network involved in body-part specific triggering of visuospatial attention

The specific behavioural association between distracting and acting body parts found in Crostella et al. (2009) studies laid the foundations for data-driven exploration of the neural underpinnings of this “somatotopic mapping”.

In the first study we used neuroimaging technique (fMRI) to explore whether specific nodes of the dorsal fronto-parietal network involved in body-part specific triggering by visuospatial attention play a specific role during saccadic and pointing tasks. Human neuroimaging studies show that perception of social attention recruits a widely distributed network, involving temporal areas implicated in face perception (i.e. Fusiform Gyrus and STS), fronto-parietal attentional regions (i.e. SPL, FEF) and areas implicated in emotion and social cognition (i.e. Amygdala and mPFC). Respectively, these regions are thought to underlie visual analysis of social attention direction, imitative attention shifts, emotional reactions and mental state attribution (Nummenmaa and Calder, 2009). Here, we predict that although fully task-irrelevant, incongruent distracters activate Fronto-parietal networks according to “somatotopic” body-matching. In particular, we anticipated a greater blood oxygenation level-dependent (BOLD) activity in those fronto-parietal nodes specifically involved in the “visual” and the “execution” processing of social stimuli with biological relevance. So, we targeted regions of interest such as, Inferior and Superior Parietal Lobule (SPL, IPL) and Frontal Eye Fields (FEF) with the objective to answer to key question such as: “Are there nodes of the fronto-parietal network specifically involved in body-part triggering of visuospatial attention and playing a specific role during saccadic and pointing tasks?”

Current literature reports that activity in the FEF has been one of the most consistent cortical correlates of social cognition in imaging studies (Mundy, 2003; Mundy and Newell, 2007). Cumulative evidence for the role of the dorsolateral prefrontal cortex, including FEF, in unwanted reflexive saccade inhibition, short-term spatial memory and prediction suggests that this area controls decisional processes governing oculomotor behaviour (Pierrot-Deseilligny et al., 2004). Indeed, the self-control of directional gaze by the FEF, and the effects of that eye gaze on the behaviors of other people, may be among the first sources of information to generate an awareness of self-intentioned action for many infants. If self-awareness of intentional action is vital to understanding intentional action in others, then systems controlling intentional visual attention may be expected to make a primary contribution to social cognition. Furthermore, clinical and brain imaging studies strongly suggest that a segregated pattern of effector representations in the Parietal Lobe is present in humans (De Renzi, 1982; Jeannerod, 1986; Pause et al., 1989; Seitz et al., 1991). It is generally accepted that a fundamental role of the parietal lobe is also to describe objects for action (Jeannerod, 1994; Jeannerod et al., 1995; Milner and Goodale, 1995). This "pragmatic", action-orientated object description has been contrasted with the "semantic" description coded in the inferotemporal lobe (Milner and Goodale, 1995; Jeannerod et al., 1995). Buccino and colleagues (2001) indicated that a "pragmatic" analysis is also carried out when an individual observes an object-directed action made by another individual. If action understanding were based on higher cognitive functions, this parietal analysis would be unnecessary. Taken together, their results strongly supported the view that during action observation there is a recruitment of the same neural structures which would be normally involved in the actual execution of the observed action. When individuals observe an action, they code that action in terms of the related voluntary movements. The “seen” actions are mapped onto the corresponding motor representations of the Frontal Lobe and, in the case of object-related actions, the “seen” objects on the effector-related, pragmatic representations, in the Parietal Lobe. This raises the possibility that a crucial fronto-parietal contribution underlying these interference effects are present when an interaction between the motor-effector (saccade vs. hand-pointing) and the category of task-irrelevant visual stimuli presented during the orienting task (eyes, hands, or non-biological cues, i.e. arrows) occurs. The present fMRI study is the first to support the evidence of a specific BOLD response preferentially modulated by a body-matching response-modality. This may also be explained in terms of “action mirroring” in a way that, the influence of spatial compatibility on imitation is highlighted by the tendency to imitate in a mirrored and spatially compatible form. This is also supported by Urgesi et al. (2006) that using TMS found an increase in corticospinal excitability during the observation of a static hand that implied a prehensile action relative to a high-level baseline (i.e. the observation of a hand in a resting position). These studies suggest that static hand stimuli are capable of activating the mirror neuron system, but only if the hand stimulus is clearly related to a hand action. This may demonstrate that reflexive shifts of attention triggered by social signals are specifically influenced by the effector used for responding. From this we aim to conclude that the social modulation of reflexive attention does not reflect mere spatial codes, but may also be mapped according to body-part specific rules.

Chapter 4

Brain Imaging Technique:
functional Magnetic Resonance Imaging (fMRI)

Functional Magnetic Resonance Imaging (fMRI) is a non-invasive neuroimaging technique allowing to study human brain function *in vivo*. Functional MRI extends the use of Magnetic Resonance Imaging to provide information about biological function in addition to the anatomical information. In the ninetieth century, Ogawa and colleagues demonstrated that by measuring the blood-oxygenation-level-dependent (BOLD) signal, fMRI could be used to visualize brain function (Ogawa et al., 1990). They attributed the contrast increase to a "*magnetic susceptibility effect"* associated with the paramagnetic deoxyhaemoglobin in red cells. The BOLD fMRI technique is designed to measure primarily, changes in the inhomogeneity of the magnetic field that result from changes in blood oxygenation, in fact it exploits the fact that haemoglobin and deoxyhaemoglobin are magnetically different. Magnetic susceptibility refers to the amount of magnetization that can be achieved when a material is placed in a magnetic field. Deoxyhaemoglobin is paramagnetic and introduces an inhomogeneity into the nearby magnetic field, while oxyhaemoglobin is weakly diamagnetic and has little effect. Thus, the paramagnetic deoxyhaemoglobin induces a susceptibility difference between the blood vessels and the surrounding tissue can be used as an endogenous contrast (i.e. depends on intrinsic property of the biological tissue) (see Figure 1).

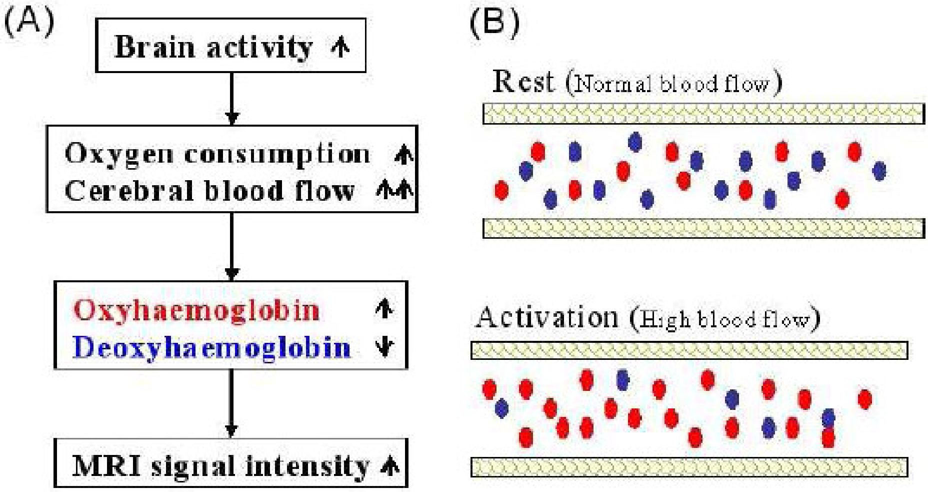


Figure 1: MR-Parameters Variation dues to the cortical activation. (A) Blood-oxygen level-dependent signal mechanism in magnetic timbre imaging. (B) oxyhaemoglobin and deoxyhaemoglobin blood flow during rest and activation (Adapted from Preuschoff K. – spm course 2010-).

Hydrogen nuclei (protons) have magnetic properties, called nuclear spin. They behave like tiny rotating magnets. In presence of a magnetic field the hydrogen atoms, present in the water molecules of the brain, align themselves with this field and reach an equilibrium state. Exchange of energy between two systems at a specific frequency is called resonance. Magnetic resonance corresponds to the energetic interaction between spins and electromagnetic radio frequency (RF). When a brief radio frequency (RF) is applied, the hydrogen atoms absorb energy (excitation) and their equilibrium state is perturbed. These hydrogen atoms would emit energy (relaxation) at the same radio frequency until they gradually return to their equilibrium state. The magnetic vector of spinning protons can be broken down into two orthogonal components: a longitudinal or Z component, and a transverse component, lying on the XY plane. Relaxation gives rise to the magnetic resonance signal and is composed of two components. Longitudinal relaxation is due to energy exchange between the spins and surrounding lattice (spin-lattice relaxation, decay constant T1) and Transverse relaxation (spin-spin relaxation, decay constant T2) occurs due to the spins getting out of phase. T1 depends on the applied magnetic field strength with longer relaxation times for greater field strengths. T2 is independent of the applied magnetic field strength and is always shorter than T1. The observed transverse relaxation time T2* is always shorter than T2 due to the combined effect of local field inhomogeneities and T2. The fundamental concept underlying the formation of a magnetic resonance image is a magnetic gradient, i.e. a spatially varying magnetic field. Lauterbur (1973) demonstrated that by superimposing a magnetic field that varies linearly across space, hydrogen atoms would precess at different frequencies in a controlled fashion. Thus different points in space become identified by different resonance frequencies. The Fourier transform of the signal would show its strength at each frequency, and thus at each position. A series of changing magnetic field gradients and oscillating magnetic fields is referred to as the pulse sequence. Presently, MRI instruments use three mutually orthogonal sets of electromagnetic 'gradient coils' to encode the three spatial co-ordinates of the MR signal (Cohen et al., 1994).

The data acquisition is achieved in two steps: First, a particular slice is selected within the total imaging volume using a one-dimensional excitation pulse. Then a two-dimensional encoding scheme (phase and frequency) is used to resolve the spatial distribution of the spin magnetizations. The field of view defines the spatial extent along different dimensions of the image space. Sequential excitation of adjacent slices may lead to off-resonance excitation (i.e. excitation of spins to intermediate state) that results in each slice being pre-excited by the previous excitation pulse. To overcome these effects, interleaved slice acquisition can be used. There are two important factors that govern the time at which MR images are collected: 1) The time interval between successive excitation pulses, known as the repetition time (TR) and 2) The time interval between excitation and data acquisition, known as echo time (TE). The most commonly used contrast for structural anatomical images is T1-weighted. A number of methods exist for contrast generation in MRI images. The T2* contrast forms the basis of BOLD fMRI. T2* contrast requires long TR and medium TE and the MR signal needs to be generated using the magnetic field gradients rather than using the refocusing pulse that would eliminate field inhomogeneity effects. Due to the reduced T2* sensitivity, spin-echo sequences are less frequently used for BOLD fMRI. The measured RF signal decays over time depending on many factors including the presence of inhomogeneities in the magnetic field. Greater inhomogeneity results in decreased image intensity. The increase in neuronal activity in a brain area results in an initial increase in oxygen consumption. After a delay of about

2 sec, a large increase in localized cerebral blood flow is triggered, which over-compensates the oxygen consumption.

Therefore, localized increases in blood flow increase blood oxygenation and consequently reduce deoxyhaemoglobin. As a result, better visibility in MRI images is thought to correlate with neuronal activity. Simultaneous fMRI and electrophysiological recordings by Logothetis and colleagues (Logothetis et. al. 2001) have confirmed that the BOLD contrast mechanism directly reflects the neural responses elicited by a stimulus. However, fMRI activation in an area is correlated with the local field potentials reflecting processing of the incoming input rather than the spiking activity. Hence, the absence of an FMRI signal does not necessarily mean that no information processing is taking place in a particular brain area. After fifteen years of fMRI studies, there is still much to learn about the source of these signals (See Heeger and Ress, 2002 for review).

4.1 Advantages and disadvantages of fMRI technique

The fMRI provides a non-invasive method to access indirectly neuronal activity in the brain with a relatively good spatial and temporal resolution. Before the emergence of functional MRI, radio isotope based techniques such as Positron Emission Tomography (PET) which measures regional cerebral blood flow (rCBF), were widely used for mapping the brain function. However, these techniques are invasive and have a low spatial and temporal resolution. Although animal studies provide an unprecedented approach to study neural mechanisms at cellular level, the limited communication and cognitive capabilities restricts the investigation of brain function in animals. Electrophysiological methods due to their invasive nature (i.e. require insertion of electrodes directly into the brain) have limited use for studying brain function in humans. Electroencephalography (EEG) measures of the electrical activity of the brain by recording on a millisecond time scale from electrodes placed on the scalp. The magnetoencephalography (MEG) and EEG techniques signals derive from the net effect of ionic currents flowing in the dendrites of neurons during synaptic transmission. While EEG has poor spatial resolution, MEG technique promises good spatial and temporal resolution. The inverse problem of uniquely identifying the locations of neural sources giving rise to pattern of activity on the skull has by and large limited the value of EEG and MEG in mapping brain function. Lesion studies provide clear evidence that a brain region is necessary for a particular behaviour but do not specify the time course of the region's activity. Lesion studies result in a permanent loss of a brain region, thus lending itself to be an irreversible process. Hence, human lesion studies can only be done by finding patients with isolated damage to a particular brain area. The temporary interruption of function within a brain region is possible using transcranial magnetic stimulation (TMS) (See Figure 2).

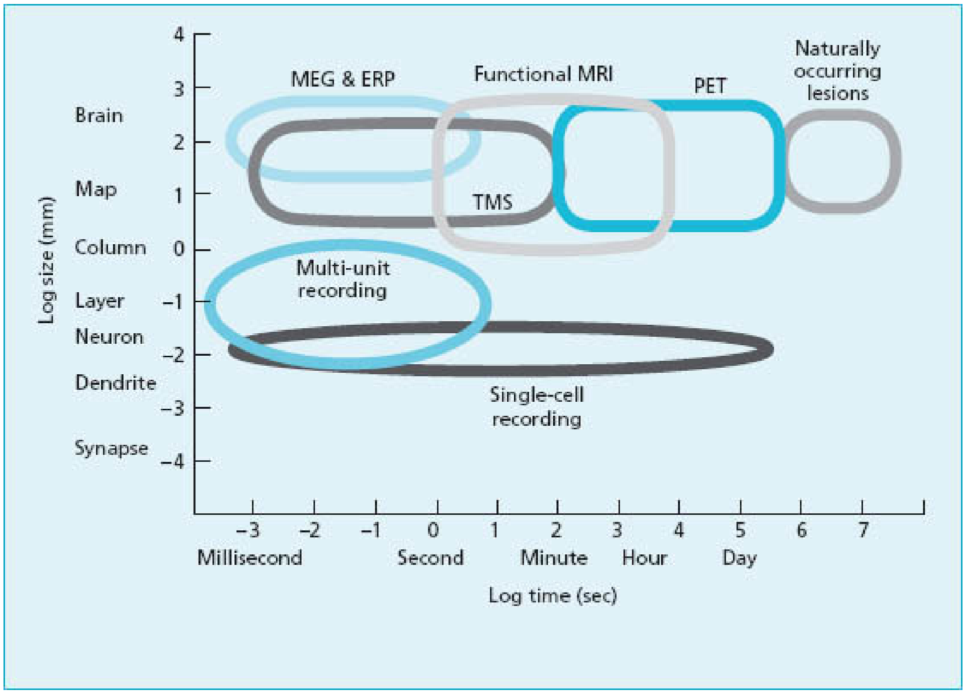


Figure 2. Methods of Cognitive Neuroscience. Cognitive neuroscience techniques can be categorized according to their spatial and temporal resolution. (Adapted from Churchland and Sejnowski, 1988).

4.2 Experimental Designs and theoretical assumptions

Although fMRI technique offers a suitable method for investigating human brain function, fMRI experiments requires careful attention to experimental design, data acquisition techniques, and data analysis (Chein and Schneider, 2003). Experimental design is at the heart of any cognitive neuroscience investigation. Because fMRI does not measure absolute neural activity, neuroimaging studies must be designed to quantify relative changes of activity. Further, the brain is constantly engaged in several controlling tasks such as respiration or heart-beat. Hence, to measure specific task-related activity, we need to scan subjects while at rest or while performing a simple baseline task (Gusnard and Raichle, 2001). Assuming that brain activity scales in a linear fashion and that cognitive processes are additive, we can test for brain activations pertaining to certain cognitive processes (Berns, 1999). Although there is no inherent baseline associated with the blood oxygen-level-dependent (BOLD) signal (Gusnard and Raichle, 2001) that is measured in fMRI studies, researchers often have attempted to establish such a baseline by using periods of rest (10- to 30-s long blocks of rest or fixation, in a blocked fMRI experiment), the final seconds of long intertribal intervals (ITIs; in the case of slow, or non-overlapping, event-related fMRI), or 2- to 4-s null trials (in the case of rapid event-related fMRI). Because no task is being performed during rest, it has seemed reasonable to assume that this baseline represents something akin to a zero-activity condition that then can be compared with activity during cognitive tasks. Therefore, when activity in a particular region of the brain during a cognitive task is no greater than during rest, it often has been supposed that this particular region of the brain is not involved in the task. Overall, designs can be classified into three types: 1) categorical, 2) factorial or 3) parametric (Friston, 1997). The categorical designs assume that the cognitive processes can be portioned into sub-cognitive processes. That is one can remove and add different cognitive processes by the assumption of *"Pure insertion"*. This assumption requires that one cognitive component does not affect the effect of another cognitive component. The categorical designs are further divided into subtraction or conjunction type. Cognitive subtraction designs are used to test the hypothesis pertaining to activation in one task as compared to that in another task considering the fact that the neural structures supporting cognitive and behavioural processes combine in a simple “additive manner”. Whereas in the cognitive conjunctions type designs, several hypotheses are tested, asking whether all the activations in a series of task pairs are jointly significant. Cognitive conjunctions can be thought as an extension of the subtraction technique in the sense that they combine a series of subtractions. While cognitive subtraction studies are designed such that a pair of tasks differ only by the processing components of interest, cognitive conjunction studies are designed such that two or more distinct task pairs each share a common processing difference. The problem of finding a baseline that activate all cognitive processes except the process of interest can be overcome by conjunction design (Price et al., 1997). The only constraint on selecting the baseline is that the component of interest is the only process that differs in each task pair (Price and Friston, 1997). Factorial designs involve combining two or more factors within a task and looking at the effect of one factor on the response to other factor. The problem of interactions (i.e., the effect that the added component in the activation task has on pre-existing components) can be overcome when the experimental design is factorial. Price et al. (1997) demonstrated that when the design is factorial, conjunction analysis reveals commonalities in activation, while the interactions reveal task-specific effects. In particular, the effect of a cognitive component (i.e., an effect that is independent of other components) is best captured by the main (activation) effect of that component and that the integration among components (i.e., the expression of one cognitive process in the context of another) can be assessed with the interaction terms (Friston et al., 1996). In parametric designs, rather than assuming that the cognitive processes are composed of different cognitive components, they are considered as belonging to different psychological dimensions. The systematic changes in the brain responses according to some performance attributes of task can be investigated in parametric designs. In parametric designs one can also look at the linear and non-linear types of relations to be determined empirically.

An fMRI experiment to test a given biological hypothesis must be designed within the constraints of the temporal characteristics of the BOLD fMRI signal and of the various confounding effects to which fMRI signal is susceptible. Typically, two designs are possible 1) Epoch-based design using Blocks of stimulation (boxcar designs with alternating activation and rest) and 2) Event-related design, where data may be recorded to monitor the BOLD response following a marked (pre-determined) event such as a single stimulus or task. Blocked design (Epoch-based) experiments are used mainly to average across many trials to obtain sufficient signal-to-noise ratios to generate functional activation images. The block design experiments descended from the low temporal resolution imaging based on blood dynamics such as PET. However, such blocked trial procedures do not allow separate trials within the task blocks to be distinguished. Blocked-designs cannot be used if we want to consider trials that depend on subject's performance (e.g. correct or wrong; chooses among different alternatives) or need to present trials in a non-blocked fashion (e.g. the oddball paradigm). It is shown that the haemodynamic response is delayed and lasts for several seconds even for brief stimulation (less than couple of seconds). As the haemodynamic response to individual trials extends temporally, the responses to successive trials may overlap. Hence the inter-trial interval between successive trials needs to last for about 15 seconds. However this severely limits the number of trials, which can be averaged per unit time, thus limiting the achievable signal-to-noise ratio. The haemodynamic response to successive events adds in an approximately linear fashion even at relatively short inter-trial intervals (2 sec and 5 sec) and hence selective averaging of rapidly presented individual trials is feasible. The findings of Dale (1997) support the Linear Time Invariant model for the haemodynamic response function. Dale has shown that the statistical efficiency of rapid event-related designs when the inter-trial interval is appropriately jittered can be up to 10 times greater than fixed inter-trial interval designs. Further, random intermixing of trial types eliminates strategy effects that might otherwise confound the results in blocked task paradigms. In conducting a hypothesis-based experiment, we wish to be able to attribute any observed effects to experimentally manipulated conditions. This can be guaranteed only if conditions are randomly allocated to a presentation order for each subject in a sensible manner. Further, this randomisation should be appropriately balanced, both across and within subjects. With such random allocation of conditions, any unexpected effects are randomly scattered between the conditions, and therefore do not affect the designed effects.

4.3) Data analysis and Statistical Parametric Mapping (SPM)

The main issue in analysing functional MRI images is comparing images, or groups of images, in a statistically meaningful way. In a typical fMRI experiment, a whole-brain functional image is acquired every 2-3 seconds resulting in a few hundred images to be analysed. Each image is acquired as a number of slices (e.g. 21 with thickness ~ 5 mm) with a typical in-plane resolution of 3x3 mm for a field of view of 192x192 mm. With these typical parameters, a single fMRI image would have dimensions of 64x64x21 mm. Statistical Parametric Mapping (SPM) is a form of data reduction, condensing information (in a statistically meaningful way) from a number of individual scans into a single image volume that can be more easily viewed and interpreted. Usually a univariate approach is followed in which the parametric map is computed by examining every voxel location across all images. In order to select a particular statistical distribution models (e.g. Poisson, normal, Gaussian), we need to know the underlying distribution of variance of the data being analysed, which is usually unknown in neuroimaging data. Further, univariate statistical models generally assume independent data points.

Several pre-processing steps are required before proceeding with statistical analysis in order to reduce artefacts and noise and to perform spatial transformations. The analysis of fMRI data within the framework of SPM5 software (http://www.fil.ion.ucl.ac.uk/spm Wellcome Department of Imaging Neuroscience, London) required several pre-processing steps.

First, spatial transformations are important in many aspects of functional image analysis and involve both within- and between-subject registration followed by spatial smoothing with a Gaussian kernel. The first several steps put each image volume into a standardized spatial reference frame. The last pre-processing step applies a Gaussian spatial filter. Usually, four scans at the beginning of each session are discarded to account for transients in magnetic field of scanner. The origin of the images is set to match the line joining anterior-commissure to the posterior-commissure (AC-PC line). The 3-dimensional functional brain images are usually acquired as a number of slices in 2-dimensions. Hence, there will be a time difference approximately equal to the TR (repetition time or inter scan interval) between the first slice and the last slice acquired in a single whole-brain acquisition. One option to compensate for the time difference between bottom and top slices of the brain is to acquire the slices in an interleaved fashion. Hence all odd numbered slices are acquired first followed by even numbered slices. During pre-processing stage, it is desirable to temporally interpolate the slices so that it would be equivalent to acquiring the whole brain image at a single time point. This is usually done with respect to a reference slice (e.g. middle slice of the brain), which depends on the regions of particular interest for a given experiment. This procedure is referred to as slice-timing correction. In functional imaging, the signal changes due to any haemodynamic response can be small compared to signal changes that can result from subject motion. So, prior to performing the statistical tests, it is important that the images are as closely aligned as possible. Although the subjects are asked to keep their head's still, movement does occur. The realignment algorithm follows a rigid-body registration procedure (Friston et al., 1995a). A rigid body can have a linear translational movement or a rotational movement in each of the three directions (X, Y and Z). Correspondingly, there are six parameters that need to be estimated (X, Y, Z translations, pitch, roll and yaw). For multi-session data, realignment works in two steps. First, the first functional images from each session are realigned to each other taking the first session as reference. Second, the remaining images within each session are realigned to the first image. As a consequence, all images are realigned to the first image from the first session. When applying slice-timing correction and realignment, the order of these two pre-processing steps needs special consideration. Applying realignment procedure first would account for large movements, but the images will no longer correspond to the specific time that the slice was supposed to have been acquired after being realigned. On the other hand, slice-timing correction essentially interpolates the data temporally and the realignment procedure would need to work on resliced images after the slice timing correction has been applied. The disadvantage of reslicing the data several times during the pre-processing stage would incur loss in the image quality. The movement-related activation can be substantially large compared to the task-related BOLD changes. Hence, often the realignment parameters are included as covariates of no interest in the statistical analysis stage. Sometimes, it is desirable to warp images from a number of individuals into roughly the same standard space to allow signal averaging across subjects. A further advantage of using spatially normalized images is that activation sites can be reported according to their coordinates within a standard space such as the one described by Talairach and Tournoux (1988). SPM5 uses the average brain template created by the Montreal Neurological Institute, that is an average of 152 brain images and hence more representative of the population as compared to the Talairach and Tournoux atlas. The Normalization process (Friston et al., 1995a) not only considers the rigid-body transformations but also considers shears and zooms to match the individual subject's images to the template. For accurate normalization, it would also be required to use nonlinear transformations that would account for deformations that do not vary in a linear fashion. SPM5 uses cosine basis functions as part of nonlinear transformations for normalization procedure. The normalization procedure usually can be performed by taking the mean functional image from the output of realignment procedure to match with the EPI template image in the MNI space and then the resultant parameters can be applied to all the functional images to be normalized. The matching of the brains in the Normalization step is only possible on a coarse scale, since there is not necessarily a one-to-one mapping of the cortical structures between different brains. Because of this, images are smoothed prior to the statistical analysis in a multi-subject study, so that corresponding sites of activation from the different brains are superimposed. Smoothing generally increases the signal relative to noise. From the matched filter theorem, to get optimum resolution of signal from noise, we need a filter that is matched to the signal. Since, haemodynamic responses are modelled to have a Gaussian shape; we need to use a Gaussian kernel of size at least twice the voxel size (FWHM of about 8 mm) for smoothing the functional images. The idea of smoothing is to replace the intensity value within each voxel with a weighted average (as determined by a Gaussian kernel centred on that particular voxel) that incorporates the intensity values of the neighbouring voxels. Smoothing is performed to compensate for residual between-subject variability after normalization. Smoothing also permits the application of Gaussian random field theory at the statistics inference stage.

After pre-processing, the images are ready for statistical analysis. FMRI data are high-pass filtered to remove physiological effects such as heartbeat, respiration, scanner-drift etc. Statistical analysis corresponds to Statistical Parametric Mapping (Friston et al., 1995b) using the General Linear Model (GLM) and theory of Gaussian fields. The GLM is used to specify the conditions in the form of a design matrix, which defines the experimental design and the nature of hypothesis testing to be implemented. The hypothesis is framed as a design matrix model. The design matrix has one row for each scan and one column for each effect one has built into the experiment or explanatory variables that may confound the results. The columns of the design matrix correspond to experimental conditions of interest (the hypothesis under test) and a set of columns that model effects of no interest. This is the stage where the groups designated for the images are specified. This stage corresponds to modelling the data in order to partition observed neurophysiological responses into components of interest, confounds, or components of no interest and an error term. GLM is an equation, which expresses the observed response variable in terms of a linear combination of explanatory variables plus a well-behaved error term. Commonly used parametric models, such as linear regression, t-tests and analysis of variance (ANOVA) are special cases of the general linear model. The GLM relates what one observes, to what one expected to see, by expressing the observations (response variable Y) as a linear combination of expected components (or explanatory variables x) and some residual error (ε), thereby equivalent to linear regression.

$$\begin{bmatrix} Y_1 \\ \vdots \\ Y_j \\ \vdots \\ Y_J \end{bmatrix} = \begin{bmatrix} x_{11} & \cdots & x_{1l} & \cdots & x_{1L} \\ \vdots & \ddots & \vdots & \ddots & \vdots \\ x_{j1} & \cdots & x_{jl} & \cdots & x_{jL} \\ \vdots & \ddots & \vdots & \ddots & \vdots \\ x_{J1} & \cdots & x_{Jl} & \cdots & x_{JL} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \vdots \\ \beta_l \\ \vdots \\ \beta_L \end{bmatrix} + \begin{bmatrix} \varepsilon_1 \\ \vdots \\ \varepsilon_l \\ \vdots \\ \varepsilon_L \end{bmatrix}$$

This can be expressed in the matrix form as:

$$\mathbf{Y} = \mathbf{X}\,\boldsymbol{\beta} + \boldsymbol{\varepsilon}$$

Here, X is called the design matrix that contains the explanatory variables and β is the unknown parameter to be estimated. The ordinary least squares approach to calculate parameter estimates β would be

$$\beta^* = (X^T X)^{-1} X^T y$$

The fitted response would be $Y = X\,\beta^*$ and the residual is y-Y. The assumption underlying least squares approximation is that the residuals are drawn from independent and identically distributed normal (Gaussian) distribution (white noise). This assumption is violated by the fMRI data, which are typically correlated from one scan to the next. Hence the effective degrees of freedom (df) cannot be assumed to be number of scans minus the dfs used in the model. SPM5 uses the restricted maximum likelihood (ReML) approach to estimate the non-sphericity (of which autocorrelation is one type) in fMRI data. MRI gives us the blood flow signal, but we are interested in the neural activity. It is possible that the neural response is quicker and the changes in blood flow take place a little later. To account for these and to find the neural activity from the MRI signal, the columns of the design matrix are convolved with the canonical haemodynamic response function (HRF). The temporal and dispersion derivatives of the HRF are used additionally to account for variation in onset and width, respectively, of the HRF across different brain regions. Brain activity specific to task is obtained by specifying linear contrasts. A contrast can be used to compare different conditions. The subtractive approach assumes that brain activity scales in a linear fashion. The conditions of interest are given a positive value, such as 1, and conditions that are to be subtracted from these conditions of interest take on a negative value, such as -1. The end result is a statistical parametric map. The activations thus obtained can be overlaid or rendered onto the high-resolution anatomical image of the subject in order to accurately locate the neural activity. Statistical parametric mapping approach is a univariate approach. That is each voxel is analysed separately. Hence for a statistical threshold of $p<0.05$, 5% of the voxels would show activation by chance alone (false activation – type I error). This means a correction for multiple comparisons is needed. The traditional way of doing this is to use some version of a Bonferroni correction. However, due to large number of voxels involved, a straightforward implementation would severely reduce the estimated number of degrees of freedom. The individual voxels in most neuroimaging modalities (PET, fMRI, EEG, MEG etc.) are heavily correlated with neighbouring voxels. Hence, to the extent that the image data approximate a random Gaussian field, correction for multiple comparison need to be only made for number of voxels that can be resolved independently (resolution elements or resels). The correction for multiple comparisons is controlled for family-wise error (FWE) rate. This assumption of random Gaussian field is assured by applying a Gaussian smoothing filter in the pre-processing stages. A serious limitation of correcting for multiple comparisons is that the number of false negatives (type II error) is increased. Another approach is to determine the false discovery rate (FDR) that controls for 5% at ($p<0.05$) of observed activations can be false positives. The FEW approach controls for a 5% chance of a single false positive. As a trade-off to correction for multiple comparison, alternative approaches have been described such as (i) using a strict uncorrected threshold (e.g. $p<0.001$), (ii) using an inference over the cluster size, so that it is unlikely to find activations in a cluster of size, say 30 voxels. (iii) small volume corrections in regions where a prior hypothesis exists (iv) a region of interest (ROI) analysis in which the average signal for all voxels in an anatomical or functional ROI is used, hence reducing the number of multiple comparisons voxel space to the number of ROIs.

In order to make an inference about brain activity in a task, the contrast images from a group of subjects are analysed using a random effects model (Holmes and Friston, 1998) using student's t-test or ANOVA like methods. The contrast images represent spatially distributed images of the weighted sum of the parameter estimates for a particular contrast. In essence, it's like a difference image for (activation-rest) or (reward-no reward). When using a one-sample t-test, one contrast image for each subject is required. By doing that, the images are being collapsed over intra-subject variability (to only one image per contrast per subject) and the image-to-image residual variability is now between subject variance alone. When using ANOVA, a number of contrast images are entered from each subject. These need to be corrected for non-sphericity. If the contrast images being entered into ANOVA are main effects of a condition, a within-subjects model should be used. On the other hand, if the contrast images have already accounted for within-subject variability, then an ANOVA without constant term can be used. The purpose of the Random Effects analysis is to find the areas that are activated in much the same way in all subjects, as opposed to a fixed effects model, which gives areas that are activated on the average across the subjects. This is really a crucial difference since a fixed effects analysis may yield significant results when one or a couple of subjects activate a lot even though the other subjects do not activate at all. The Random Effects analysis incorporates both within-subject variance, as well as between-subject variance. This allows generalization of the results to the population from which the subjects were drawn.

Chapter 5

Mapping reflexive shifts of attention in eye- and hand-centred coordinate systems

Experiment 1

Introduction

Allocation of attention to a specific point in space may be automatically triggered by biological (e.g. averted gaze or pointing hands) as well as non-biological directional signals (e.g. regulatory or warning road arrows) (for a review see: Itier and Batty, 2009; Frischen et al., 2007; Langton et al., 2000). Whether biological cues are pre-eminent in determining attentional shifts with respect to non-biological cues is hotly debated (Friesen and Kingstone, 1998; Friesen et al., 2004, 2005; Hietanen, 1999; Jonides, 1981; Tipples, 2002; Eimer, 1997; Ristic et al., 2002, 2007; Bonato et al., 2009; Stevens et al., 2008), mainly because laboratory based paradigms use impoverished tasks that hardly reproduce the situational complexity of real life human interactions (Kingstone, 2009; Birmingham and Kingstone, 2009). Indeed, fundamental socio-cognitive operations, e.g. intention and mind reading, are inherently linked to the power of gaze in capturing the attention of an observer and in triggering reflexive joint attention under daily life conditions (Smilek et al., 2006; Kuhn and Land, 2006). Possibly because eye contact is a hallmark of interpersonal interactions, a considerable number of behavioral studies focused on the role of gaze perception in modulating social attention (for a review see: Nummenmaa and Calder, 2009; Kingstone, 2009; Klein et al., 2009). Importantly, unlike non-social orienting cues such as arrows, gaze cues not only signal a seen agent's direction of attention but are also used to infer current goals and intentions of other individuals. This difference raises the important issue, explored by recent functional neuroanatomy and electrophysiological studies, of whether orienting attention to biological, socially relevant cues, such as gaze, may engage neural mechanisms distinct from those engaged by orienting to non-social cues. Hietanen et al. (2006), for example, explored at behavioural and neural levels the effect of responding to left or right visual targets preceded by central non-predictive gaze or arrow cues pointing to same or opposite direction. While the interference effects of cue-target directional incongruence was found for both gaze and arrows, changes of BOLD signal revealed that while gaze-cued orienting recruits occipital regions, arrow-cued orienting also recruits parietal and frontal regions. That arrow-cues related orienting activates a larger network with respect to gaze-cue related orienting is also suggested by an event- related potential study showing that changes of parietal and frontal attention-directed neuroelectric signatures are found for arrow- but not for gaze-cues (Hietanen et al., 2008). However, using an ingenious event-related fMRI design in which the central cue was an ambiguous stimulus that could appear as an eye in profile or an arrow, Tipper and colleagues (2008) demonstrated that attention to social and nonsocial cues activates a largely overlapping neural network centered upon ventral and dorsal fronto-parietal and lateral occipital regions. Since activation in two regions of this network, namely the ventral frontal cortex and the lateral occipital, was higher for gaze- than arrow-cues, the suggestion was made that quantitative more than qualitative differences underlie the social vs. non-social mapping of attentional shifts (Tipper et al., 2008).

Although most of the original studies focused on the importance of gaze in social attention, body parts other than the eyes play a fundamental role in triggering joint attention. Studies demonstrate, for example, that full body/head orientation as well as hand orientation of a model modulates attentional shifts of an observer (Langton, 2000; Langton and Bruce, 2000; Pierno et al., 2008). Much less is known on whether shifts of attention are similarly triggered by different person-related cues. Information on whether reflexive social attention triggered by different person-related cues is mapped according to the social valence of the cue or in body-centered coordinates is very scanty. Studies indicate that social attention may recruit a more extensive neural network with respect to non-social spatial attention. Indeed, areas involved in face, gaze, hand and even full body perception may be called into play specifically in social attention tasks (Nummenmaa and Calder, 2009). This raises the question of whether social spatial attention may be coded according to body-centered coordinate systems. In a recent behavioral study, we explored whether the interference effect of person-related cues (averted gaze and pointing hands) and of non-social stimuli (arrow) was specifically influenced by the type of effector used for responding namely, saccadic movements and hand pointing (Crostella et al., 2009). We expected that a non-specific spatial interference of social stimuli would produce higher interference of gaze and pointing hands than arrows, regardless of the body part performing the action. By contrast, we hypothesized that finding a relation between the type of distracting stimulus and the type of response would suggest that additional reference frames are called into action in the task. The results showed that distracting gaze stimuli interfere specifically with saccadic performance and distracting hand stimuli with pointing performance. Relevant to this issue is the fMRI study showing that mere observation of directional and non-directional eyes, hands, and arrows in the absence of any motor response, activated overlapping neural regions that included the posterior superior temporal sulcus (STS), the inferior parietal lobule (IPL), the inferior frontal gyrus (IFG), and the occipital cortices in the right hemisphere (Sato et al., 2009). Capitalizing on such behavioural and neuroimaging evidence we sought to determine whether the neural activity in the network underpinning the observation of person- and non-person related signals was modulated by the relationship between type of distracter and type of effector used for the response. We recorded changes of BOLD fMRI signal associated to conditions where three different distracters (gaze, hand or arrows) influenced overt directional saccadic or hand responses triggered by central instruction signals. This design allowed us to highlight: i) the neural network activated during reflexive shift of attention triggered by social and non social distracters; ii) the possible modulatory role of gaze and hand distracters on saccadic and hand pointing responses, respectively. We predicted a specific involvement of dorsal frontoparietal structures in modulating attentional shifts triggered by directional, socially relevant stimuli (i.e. eyes and hand vs. arrow). The fronto-parietal attention system, which includes portions of the intraparietal cortex (e.g. the intraparietal sulcus, IPS) and of the superior frontal cortex (e.g. frontal eye field, FEF) (Corbetta et al, 2002), is involved in the selection of stimuli and goal-directed responses for goal-directed actions. Importantly specific sections of this system (FEF and some parts of IPS) may be differentially active when subjects plan and perform visually guided hand movements, instead than eye movements (for a review see Corbetta and Shulman, 2002; Corbetta et al., 2008; Astafiev et al., 2003). It is also relevant that clinical and brain imaging studies suggest the presence in humans of a segregated pattern of effector representations in the parietal lobe (De Renzi, 1982; Jeannerod, 1986; Seitz et al., 1991).

Based on this evidence we investigated whether the tendency of an onlooker to imitate the actions of the observed model reflects the activity of a resonant system that works according to body-part specific reference frames.

Materials and Methods

Participants

Eighteen right-handed volunteers (10 males - 8 females, mean age = 28 years, range: 23-36 years) took part in the study. All subjects had normal or contact-corrected-to-normal visual acuity. All were in good health, free of psychotropic or vasoactive medication, with no history of psychiatric or neurological disease. After having received an explanation of the procedures, participants gave their written consent. The study was approved by the independent Ethics Committee of the Santa Lucia Foundation (Scientific Institute for Research Hospitalization and Health Care). Behavioural and imaging data were analyzed for subjects who showed reliable interference effects (slower responses for incongruent vs. congruent condition both for saccade and pointing task). Five subjects did not meet this criterion and therefore were not included in the analyses that were performed on thirteen subjects (8 males, mean age: 27.5 years; 5 female, mean age: 27 years; range: 23-32 years).

Stimuli and Procedure

Participants were positioned in the scanner, in a dimly lit environment. The experimental visual stimuli were presented via a mirror mounted on the MRI headcoil (total display size 19.5° x 14.6° degrees of visual angle, 1.024 × 768 screen resolution, 60 Hz refresh rate). The visual stimuli were back-projected on a screen behind the magnet. Stimulus presentation was controlled with Cogent2000 (www.vislab.ucl.ac.uk/Cogent/).

Each trial started with the appearance of a black central fixation mark (0.5° x 0.5° in size), presented centrally against a grey background**,** and of two black squares (1.4° x 1.4° in size), presented for 500 ms at 7.5° of eccentricity in the left and the right visual field. The distracting stimuli consisted of digital Photoshop 8.0.1 (Adobe, CA) modified photographs of gaze, hand or arrow. The three distracters were created by using coloured photographs of: i) an emotional neutral-expression, full-face of a young woman looking to the right; ii) a man hand pointing to the right; iii) an arrow pointing to the right obtained by digitally scrambling the hand distracter. The mirror images of these pictures were created to produce leftward directed stimuli. To make the attention-capture effect conspicuous and the scenario reminiscent of what can be encountered under daily life conditions the stimuli were animated by presenting two frames in rapid sequence. The first frame depicted a straight gaze, an upward pointing fist or a T-like shape. The second frame, which depicted a left- or rightward oriented gaze, extended finger or arrow, replaced the first frame. The direction of the distracter and the one indicated by the instruction-cue could be 50% of the time congruent or incongruent. Before starting the fMRI acquisition each participant was asked to perform outside the scanner a training task in which they had to learn with 100% accuracy on 30 consecutive trials per task, the association between instruction signal (red or blue) with leftward or rightward saccadic or pointing movements.

In the scanner, each trial started with the presentation behind the black fixation mark of a straight gaze, an upward pointing fist or a T-like shape which lasted 500 ms. At 500 ms, a second frame, that depicted left- or rightward oriented gaze, extended finger or an arrow, replaced the first frame and created a strong animation effect. The directional distracters remained on until the end of the trial. 75 ms after the oriented distracter presentation, the black central fixation mark (imperative-cue) changed to either blue or red colour. This was the instruction signal for the subjects to make, in separate runs, a saccade or a right index pointing movement towards the left (change into red) or the right (change into blue) target square (for saccades) and the left or right button of a home-made keypad (for pointing). Thus, the direction of the distracter and that indicated by the instruction-cue could be congruent (left-red or right-blue) or incongruent (left-blue or right-red). The coloured cue remained visible until the end of the trial (See Fig 1).

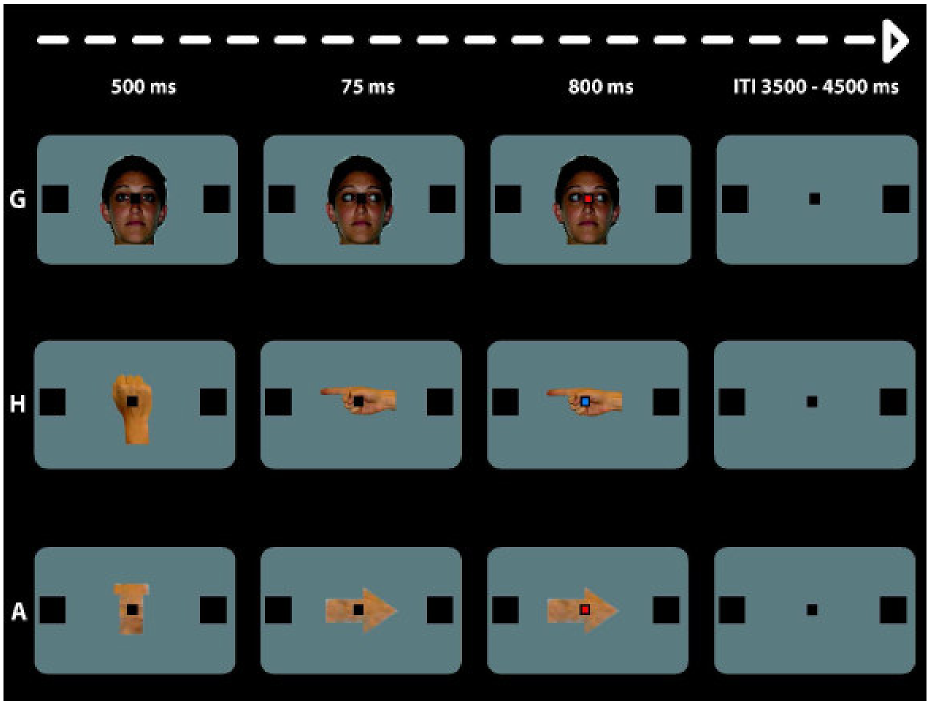


Fig 1: Schematic depiction of the events occurring during a representative trial. The three possible distracting stimuli namely: G) gaze, H) pointing hand, A) arrow, are reported. At the beginning of the trial, a straight gaze, an upward pointing fist or a T-like shape was presented behind a black fixation mark (500 ms). Turning the black fixation point into red was the imperative instruction signal for leftward saccades or hand pointing movements. Only incongruent conditions are represented for the sake of simplicity.

In order to engage automatic processes and minimize expectations, the directional cues were equiprobable (50% congruent) and non-predictive. It is worth noting that the subjects were instructed to ignore the distracters and to focus on the central mark colour change. Moreover, they were explicitly informed that the instruction cue was not informative on the direction of the distracters. In the hand-pointing task, subjects were also instructed to fixate the central cross for the entire trial. This allowed us to measure attentional shifts independent of eye movements. In order to avoid subjects anticipating stimuli, a random inter-trial interval ranging from 3.5 to 4.5 s was used. Twelve event types were organized in a 3 x 2 x 2 factorial design. One factor was the *Distracter*: *gaze*, *hand* (both biological distracters with social valence) and *arrow* (non biological, non social distracter). The second factor was the type of *Effector*: *saccadic* vs. *pointing* movements. In order to minimize any task-switching requirements, each participant performed 3 fMRI runs of saccadic movement and 3 fMRI runs of pointing movement. The order of the effectors was counterbalanced across participants. On each run participants were verbally instructed about the motor response to be performed (saccadic or pointing task). The third factor was the *Condition*: *congruent* vs. *incongruent* direction between instruction signal and distracter. Congruent and incongruent directional combinations of instruction cues and distracters were presented in unpredictable and randomized order. Thus, fMRI data were acquired via a mixed, blocked (Distracter, Effector)/event related (Condition) protocol. All participants underwent six fMRI runs. Each participant completed a total of 720 trials, (360 for each effector), therefore each imaging session consisted of 40 repetitions for each of the three distracters (Gaze/Hand/Arrow), respectively 20 for congruent and 20 for incongruent conditions (balanced for left/right direction and red-blue imperative-cues). Each scanning session lasted approx. 8 min for a total experiment duration of about 50 min.

Eye movements recording

In the training session outside the scanner, subjects sat in front of a computer screen. In all subjects, eye position and saccadic movements were monocularly monitored using an infrared video camera (Sony EVI D31, color video camera, Sony JP). Participants were instructed to look at the location indicated by the instruction-cue and then to quickly look back at the fixation point. During the scanning session, again the participants' saccadic movements were monocularly monitored in real-time by means of an ASL eye-tracking system that was adapted for use in the scanner (Applied Science Laboratories, Bedford, MA; Model 504, sampling rate: 60 Hz). For each subject the eye-tracking system was calibrated before fMRI scanning. The calibration was repeated during the experiment whenever necessary. Eye-position traces were examined in a 1175 ms time window, beginning with the imperative cue onset until the end of the trial. In the sessions requiring pointing movements the maintenance of central fixation was monitored throughout the trial. We defined losses of fixation as changes in horizontal eye-position greater than ±2° of visual angle with durations at least 100 ms. For trials requiring saccadic responses (Saccadic Task), the saccadic RTs were calculated from the target onset time to when an horizontal eye position exceeded 2°. Moreover, we did not compute RTs for the trials in which subject made a saccade to the wrong side (e.g., saccade to the left target after the central cue turned into blue) or did not perform any saccade at all.

Hand movement recording

In the training session outside the scanner, participants sat in front of a computer screen by keeping their right index finger on a central response key until the occurrence of the instruction signal. Then, based on the directional instruction cue, subjects pointed towards a left or a right key located 2 cm laterally with respect to the central position. In the scanner, the right hand was positioned in correspondence of the low abdomen in a relaxed posture with the right index finger extended and all other fingers flexed. This position allowed participants to perform central-cue instructed index finger movements toward the right or the left button key. The right shoulder and arm were supported and immobilized with cushioning wedged between the scanner bed and the coil surface. When the central mark changed colour, subjects pointed as quickly as possible in the direction of the target location (lateral key presses) and then returned to the resting position. Pointing involved a minimal rotation of the wrist with extending index without movements of the shoulder or the arm (see Astafiev et al., 2003). For pointing data we computed a Release RTs measure and we only analysed trials in which subjects maintained fixation on the central fixation mark.

Magnetic Resonance Imaging

A Siemens Allegra (Siemens Medical Systems, Erlangen, Germany) operating at 3T and equipped for echo-planar imaging (EPI) acquired functional magnetic resonance (MR) images. A quadrature volume head coil was used for radio frequency transmission and reception. Head movements were minimized by mild restraint and cushioning. Thirty-six slices of functional MR images were acquired using blood oxygenation level-dependent imaging (3.0 x 3.0 x 2.5 mm thick, 50% distance factor, TR = 2.34 s, TE = 30 ms), covering the entire cortex.

Data Analysis

We used the statistical parametric mapping package SPM5 (www.fil.ion.ucl.ac.uk) implemented in MATLAB (v 7.1, The MathWorks, Natick, MA) for data pre-processing and statistical analyses. For all participants, we acquired 1.290 fMRI volumes, 215 for each run. The first four image volumes of each run were used for stabilizing longitudinal magnetization and were discarded from the analysis. Pre-processing included rigid-body transformation (realignment) and slice timing to correct for head movement and slice acquisition delay. Residual effects of head motion were corrected for by including the six estimated motion parameters for each subject as regressors of no interest. Slice-acquisition delays were corrected using the middle slice as a reference. All images were normalized to the standard SPM5 EPI template, resampled to 2 mm isotropic voxel size, and spatially smoothed using an isotropic Gaussian kernel of 8 mm FWHM. Statistical inference was based on a random effects approach (Penny and Holmes, 2004). First, for each participant, the data were best-fitted at every voxel using a combination of effects of interest. These were delta functions representing the onsets of the 12 conditions given by the crossing of our 3 x 2 x 2 factorial design: *Distracter* [gaze/hand/arrow] x *Condition* [congruent / incongruent] x *Effector* [saccadic movement / pointing movement] convolved with the SPM5 hemodynamic response function. The onset of the hemodynamic response function was aligned with the onset of the imperative cue with duration =0. Onsets of trials in which an erroneous response or an eye movement toward the wrong side occurred were included in the design matrix as covariates of no interest, but excluded from any further analysis. Linear contrasts were used to determine differential activation for incongruence minus congruence conditions separately for 3 x 2 (*Distracter* x *Effector*) (e.g. [Gaze(Incong) > Gaze(Cong)] for saccadic movement) factors, averaging the 3 fMRI runs (three for the saccade and three for the pointing task). These 6 contrasts images were entered in a 3×2 factorial ANOVA with *Distracter* [gaze, hand, arrow] and *Effector* [saccadic movement, pointing movement]. Finally, linear compounds (contrasts) were used to compare the Incongruence effect using between-participants variance (rather than between scans). Correction for nonsphericity (Friston et al., 2002) was used to account for possible differences in error variance across conditions and non-independent error terms for the repeated measures.

The analyses aimed at determining: i) the brain regions called into action when directional cue and distracters provided conflicting directional information (incongruent condition); ii) whether any modulation exerted by the biological distracters (gaze, hand) was specifically linked to the effector the onlookers used for responding; iii) whether reflexive joint attention was differentially modulated by the biological (gaze, hand) vs. non-biological distracters (arrow), irrespective of motor effector.

We first sought to determine any specific cortical attentional network associated with the directional incongruence conditions (comparing incongruent vs. congruent condition, irrespective of distracter and effector). Thus, the main effect of Incongruence allowed us to identify the network activated by the directional conflict between task-irrelevant distracters and instruction signals. For this comparison, the SPM threshold was set to *p-corr* = < 0.05 at cluster level (cluster extent estimated a *p-uncorr* = 0.001), considering the whole brain as the volume of interest. To test for the interaction between the Interference Effect (IE) with Motor-Effector and Distracter, we created regions of interest (ROIs) extracting average BOLD signals (MarsBar 0.41, ‘MARSeille Boîte À Région d'Intérêt’ SPM toolbox) from the peak activity of the voxels that showed a main effect of Incongruence. Each ROI was defined as a 10 mm radius sphere centred on the corresponding maxima of the whole-brain analysis (see table II), and p-values were Bonferroni-corrected. We expected that our manipulations of IE would affect activity within the dorsal fronto-parietal attentional systems depending on specific relationships with *Distracter* and *Effector* (Corbetta and Shulman, 2002; Crostella et al., 2009; Ricciardelli et al., 2002). Accordingly, we used a combination of anatomical and functional criteria to identify six ROIs in the dorsal attentional system: the frontal eye field (FEF), the posterior parietal cortex (PPC), the intraparietal sulcus (IPS) bilaterally. The bilateral frontal ROIs included a portion of middle frontal gyrus (FEF) located laterally to the superior frontal sulcus (Paus, 1996). Because of the large extension of parietal cortex clusters, we decided to distinguish between posterior and anterior anatomical regions, i.e. bilateral posterior parietal cortex (PPC) and intraparietal sulcus (IPS) respectively. Bilateral PPC included a portion of superior parietal lobule close to superior parietal gyrus and precuneus. Bilateral IPS ROIs were instead located more anterior and close to the inferior parietal lobule, the angular gyrus and along the intraparietal sulcus.

For each ROI, we tested the 3-way interaction *IE* x *Effector* x *Distracter* in order to provide information on whether the cost of directional incongruence was mapped on different brain regions depending on specific relationships with distracter and motor effector. For example, this interaction allowed exploring whether observation of incongruent saccades performed by the distracting gaze induced differential brain activity in the onlookers' when performing the saccadic with respect to the hand-pointing movement. It should be noted that main effect and interactions are orthogonal and, therefore, our ROI selection procedure was unbiased. Moreover, based on the prediction that interference effects are stronger when elicited by social (gaze and hand) than by non-social (arrow) distracters, we tested the interaction between the IE and the biological vs. non-biological distracters, irrespective of motor effector.

Results

Behavioural performance

Both saccadic and release mean RTs were calculated collapsing left and right target trials. Incorrect responses (movements performed following distracters instead than instruction cues), misses (no response), anticipations (RTs < 100 ms) and retards (RTs > 1.500 ms) were not included in the analysis. Overall, we discarded 12.7 % of trials for saccadic sessions and 7.5% of trials for pointing sessions. Following previous studies (Murphy and Klein, 1998; Spence et al., 2001a,b; Kitagawa and Spence, 2005), we computed an inverse efficiency score by dividing, for each condition and in each subject, the mean correct RTs by the percentage of directionally correct responses. The inverse efficiency score provides a way to combine RT and accuracy measures of performance into a single measure (Townsend and Ashby, 1983) and allows controlling for any speed-accuracy trade-off effects. As for RT and error measures, higher inverse efficiency scores indicate worse performance. Table I reports inverse efficiency scores in the saccadic and hand pointing tasks, for each distracter type and incongruent and congruent conditions, acquired during fMRI scanning.

		Distracter		
		G	**H**	**A**
Saccade	**Congruent**	512(33)	511(44)	494(30)
	Incongruent	608(56)	634(41)	648(55)
Hand pointing	**Congruent**	528(30)	511(24)	499(21)
	Incongruent	552(30)	521(25)	534(24)

Table I. Behavioural performance for Saccadic and Hand-Pointing tasks. Inverse efficiency scores (mean RT/percentage of correct responses, S.E.M. in brackets) are represented separately for saccadic and release RTs as a function of Distracter [G= Gaze / H= Hand / A= Arrow] and Condition [Congruent / Incongruent].

The inverse efficiency scores were entered in two separate 3 x 2 repeated-measures ANOVAs (one for saccadic and one for pointing task) with *Distracter* (gaze, hand, arrow), and *Condition* (congruent, incongruent) as within-subjects effects. In the saccadic task, the main effect of *Condition* (F (1,12) = 22.297, p = .001) was explained by the worse performance in the incongruent than congruent trials (629 vs. 505 ms/percentage of correct trials). No other effects or interactions were significant. Also in the pointing task, the main effect of *Condition* was significant (F (1,12) = 8.521, p = .01) because of the worse performance in the incongruent than congruent trials (535 vs. 510 ms/percentage of correct responses). Again, no other effects or interactions were significant.

To sum up, saccadic and release RTs/percentage of correct trials scores during MR scanning show that the incongruent cues worsened both saccadic and pointing performances. However, this effect was independent from the type of *Distracter* (as indicated by the non-significant *Distracter* x *Effector* interaction).

fMRI data

Main effect of Incongruence

To highlight the neural underpinnings of the interference effect triggered by incongruent distracters, we tested for the main effect of incongruence irrespective of *Distracter* and *Effector* (See table II).

Anatomical Area	**Cluster Size**	***p-corr***	**x**	**y**	**z**	**z scores**
Parietal Lobe						
R PPC	7804	< .001	14	-66	58	6.09*
L PPC			-22	-70	46	5.67*
R IPS			42	-56	58	3.97*
L IPS			-32	-44	40	4.98*
Frontal Lobe						
R FEF	930	< .001	36	0	56	5.81*
L FEF	507	< .001	-28	0	54	5.54*
R Cingulum Mid	397	< .001	8	14	46	4.16
L Precentral G	376	.002	-52	2	38	4.90
R Insula	1346	< .001	34	24	8	5.21
L Insula	564	< .001	-30	20	6	4.89

Table II. Mean MNI coordinates of activation foci associated with Incongruence Effect. Anatomical locations, peak coordinates in MNI space (Montreal Neurological Institute), and statistical values for the main effect of incongruence (incongruent > congruent trials, irrespective of distracter and effector). *p*-values are corrected for multiple comparisons at the cluster level, considering the whole brain as the volume of interest. R/L PPC= Right/Left Posterior Parietal Cortex; R/L IPS= Right/Left Intraparietal Sulcus; R/L FEF= Right/Left Frontal Eye Field; R/L Insula= Right/Left Insula; R Cingulum Mid= Right Middle Cingulum; L Precentral G= left Precentral Gyrus. With the asterisk (*) we indicated the regions of interest (ROIs) within the dorsal fronto-parietal attentional network. ROIs were extracted averaging BOLD signals (see Methods) from a 10 mm sphere centred on the cluster peak.

This contrast revealed the expected activation of the ventral and dorsal frontal and parietal regions. The parietal region consisted of a large cluster including the right superior and inferior parietal cortex bilaterally. The frontal region included the left precentral gyrus, the right middle frontal cortex bilaterally, the right supplementary motor area, the most posterior portion of the inferior frontal gyrus, the operculum, bilaterally, and the pars triangularis extending into the insula and the middle portion of the right cingulate cortex (See Fig 2).

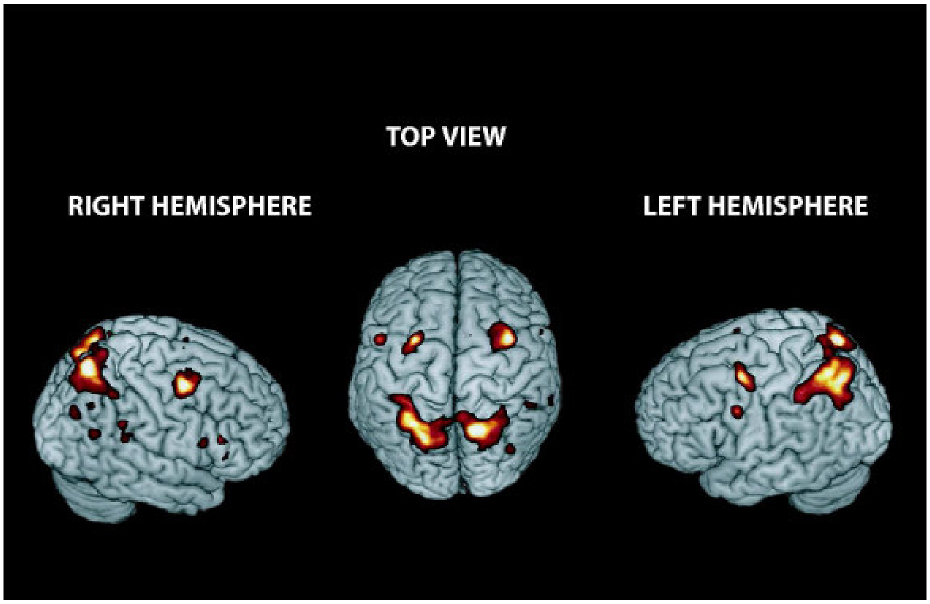


Fig 2: Brain regions activated by Incongruence [Incongruent > Congruent trials]. Clusters showing higher activity in the incongruent than congruent irrespective of distracter and effector are rendered on 3-dimensional (3D) views of the SPM template. This contrast revealed the activation of frontal and parietal regions. The frontal region included the left Precentral Gyrus (L Precentral G), the right Middle Frontal (L/R FEF) cortex bilaterally, the right Supplementary Motor Area (R SMA), the most posterior portion of the Inferior Frontal Gyrus, the Operculum, bilaterally and the Pars Triangularis (IFG) extending into the Insula and the middle portion of the right Cingulate Cortex. The parietal region included the right superior and inferior Parietal Cortex bilaterally. These regions were used as regions of interest to assess any differential influence of distracter/instruction signal incongruence on brain activity (SPM thresholds are set to *p-corr.* = 0.05 at cluster level).

The Main Effect of Incongruence considering the three distracters ([G=Gaze / H=Hand / A=Arrow], averaging across saccadic / hand-pointing motor effector) was used to define the centre of each ROI in the two hemispheres. Within each ROI, we tested for: i) the critical interaction: IE of *Distracter* (Gaze and Hand) on the paired saccadic and hand pointing task; ii) the IE of biological (Gaze, Hand) vs. non-biological distracters (Arrow), irrespective to effector.

Interference Effect of Distracters in the Saccadic and Hand Pointing Tasks

We investigated the possible influence on BOLD signal of the pairing between body-part related (gaze or pointing hand) distracter of motor-effector used for the response (eyes or hand) within each frontal and parietal ROI. The mean BOLD activation for each *Distracter* and *Effector* in the frontal and parietal ROIs is shown in figure 3. Statistics, for the interaction effect and additional t-test in each ROI are reported in table III.

		IE for Distracter by Effector		**IE for Saccade [G] >[H]**		**IE for Pointing [H] >[G]**	
Side	**Anatomical Area**	**t-test Values**	***p corr***	**t-test values**	***p uncorr***	**t-test values**	***p uncorr***
L	**FEF**	3.06	< .01	3.04	< .01	1.82	n.s.
	IPS	2.47	< .05	1.32	n.s.	2.52	< .01
	PPC	1.87	n.s.	1.43	n.s.	1.36	n.s.
R	**FEF**	2.33	.068	2.36	< .05	1.41	n.s.
	IPS	2.32	.069	0.71	n.s.	2.79	< .01
	PPC	2.33	.068	2.57	< .01	1.22	n.s.

Table III. Interference effect of Distracters in the Saccadic and Hand-Pointing Tasks. Anatomical locations of ROIs, t-test and p-values (*Bonferroni-corr*) for the Interference Effect (IE) of social distracter [Gaze= G / Hand= H] by effector [Saccade/Pointing], in the Left/Right (L / R) hemispheres. A significant interaction was found for L FEF and L IPS, while a trend toward significance was found for R FEF and R IPS. Additional t-test (*p-uncorr*) confirmed a significant larger differential effect for ([G] > [H]) distracter in the L and R FEF, while bilateral IPS showed a larger IE for ([H] > [G]) (see Results section for more details), indicating a selective correspondence between G/H body-part and saccadic/hand-pointing effector.

Left FEF was specifically modulated by the interaction *IE* x *Distracter* x *Effector*, while right FEF showed a trend toward significance. To further confirm the specificity of these effects, we compared the IE of gaze vs. hand distracter for saccadic motor effector. This revealed that left and right FEF were modulated by the selective correspondence between ‘Gaze’ body-part and ‘Saccadic’ effector (See bars figure 3, left panel**:** [G] > [H]). The opposite pattern was found in left IPS region; as for left FEF, this region resulted specifically influenced by the interaction *IE* x *Distracter* x *Effector*, while right IPS showed a trend toward significance. Additional t-test confirmed that this effect was due to a larger IE for ‘Hand pointing’ than gaze-distracter during ‘Hand pointing’ movements (See bars Fig 3, right panel: [H] > [G]).

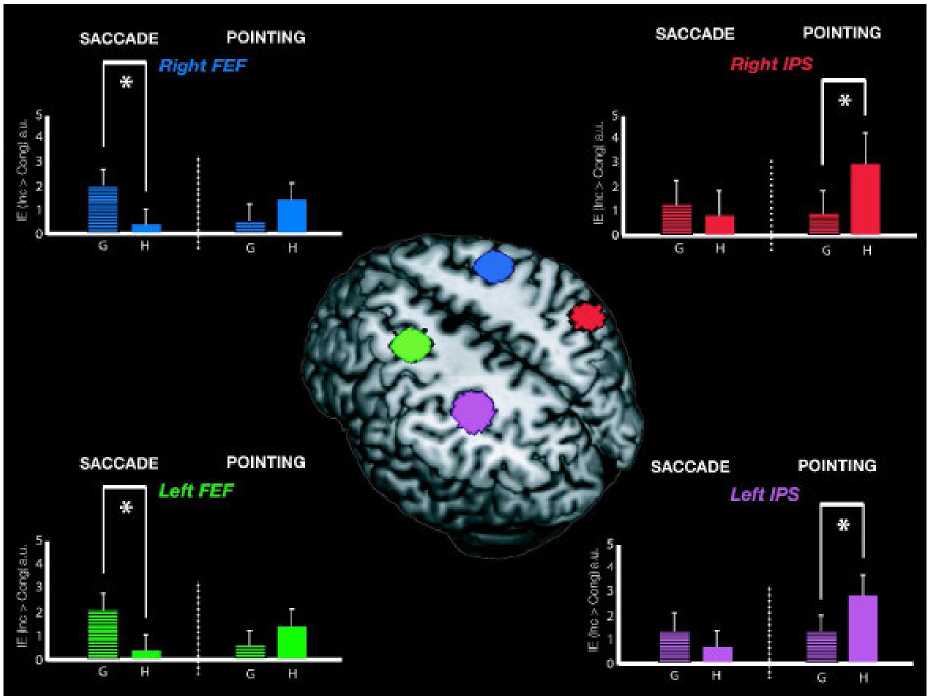


Fig 3: Activity in the bilateral Frontal Eye Field and Intraparietal Sulcus regions elicited by the Interference Effect of the two social Distracters during Saccadic and Pointing movements. Central panel: 3D rendering of the canonical MNI template showing the localisation of four regions of interest (ROI) corresponding to the left

(green) and right (blue) frontal eye fields [FEF] and to the left (pink) and right (red) Intraparietal Sulcus [IPS] is reported in the axial section. Left panel: signal plots for the Interference Effect [IE(inc>cong)] in the right FEF (up) and the left FEF (down) as a function of the two biological distracters [G=Gaze / H=Hand] and effectors [Saccade / Pointing]. Right panel: signal plots for the Interference Effect [IE(inc>cong)] in the right IPS (up) and the left IPS (down) for each biological distracter [G=Gaze / H=Hand] during saccadic and hand-pointing task. In each plot, the level of activity for the four conditions represents the average amplitude of the hemodynamic response for the [IE(inc>cong)] belonging to the corresponding condition (e.g., Gaze or Hand trials, for Saccade) and expressed in arbitrary units (a.u., ± 90% confidence interval). The asterisks indicate significant ([G] vs. [H]) difference for left/right FEF and ([H] vs. [G]) difference for left/right IPS.

This demonstrates that activity in these regions is specially influenced by the motor effectors used to perform the task. This effect was stronger in the left than in the right hemisphere. Finally, left PPC was not sensitive to this interaction given that results were not replicated (albeit a significant IE for Gaze more than Arrow was found for right PPC).

fMRI activations associated to the Interference Effect of Biological vs. Non-Biological distracters

In order to explore whether reflexive joint attention was differentially modulated by the different categories of distracters (e.g. biological and social vs. non-biological non social cues) independently from motor-effector, we compared the IE for biological (gaze and hand) vs. non-biological distracters (arrow). Statistics for the interaction effect and additional t-test in each ROI are reported in table IV.

		IE for Bio vs. Non-Bio		**IE for [G] > [A]**		**IE for [H] > [A]**	
Side	**Anatomical Area**	**t-test Values**	***p Corr***	**t-test values**	***p uncorr***	**t-test Values**	***p uncorr***
L	**FEF**	1.74	n.s.	2.03	< .05	1.09	n.s.
	IPS	3.00	< .05	2.18	< .05	2.24	< .001
	PPC	2.52	< .05	2.26	< .05	2.24	< .05
R	**FEF**	1.38	n.s.	1.52	.066	1.00	n.s.
	IPS	1.41	n.s.	0.71	n.s.	2.13	< .05
	PPC	3.07	< .01	2.82	< .01	2.74	< .01

Table IV. Interference Effect of Biological vs. Non-Biological Distracters. Anatomical locations of ROIs, t-test and p-values (*Bonferroni-corr*) for the Interference Effect (IE) of biological [Gaze= G / Hand= H] vs. non-biological distracter [Arrow= A], in the Left/Right (L / R) hemispheres. A significant interaction was found for L/R PPC and L IPS. Additional t-test (*p-uncorr*) confirmed significant larger differential effect for biological vs. non-biological ([G] > [A]) and ([H] > [A]) in bilateral PPC and L IPS, irrespective to Effector (see Results section for more details) (albeit some trends were found for bilateral FEF and R IPS). These results confirm a larger IE driven by the biological distracters with social valence, (Gaze and Hand) respect to Arrow.

Significant interactions, more predominant in the left hemisphere were found within the parietal ROIs. In particular, in the left and right PPC the activation for the IE triggered by biological distracters (gaze, hand) was larger than the activation for the IE triggered by non-biological distracter (arrow) (See Bars Fig 4: [G] > [A]).

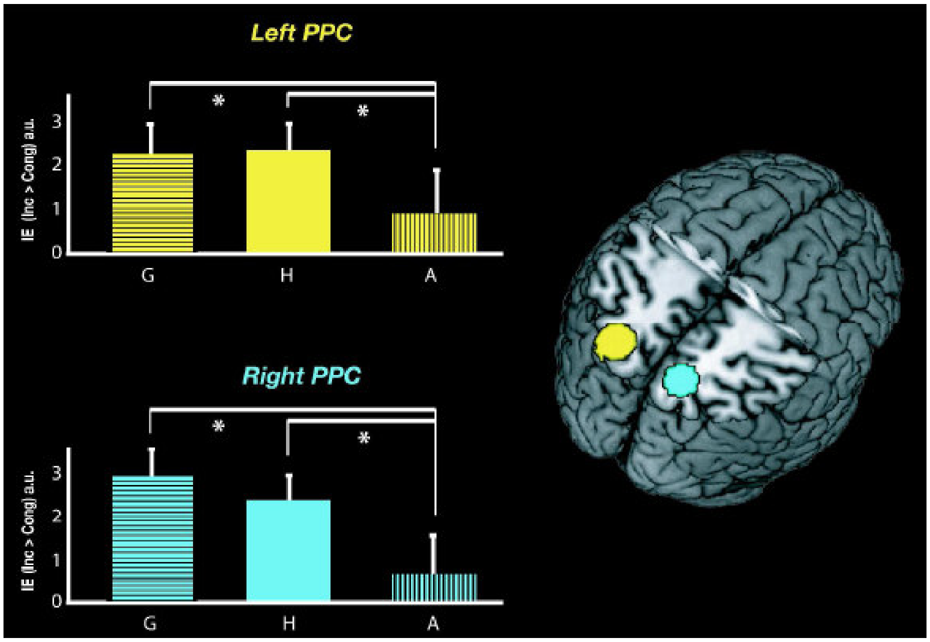


Fig 4: Activity in the bilateral Posterior Parietal Cortex regions elicited by the Interference Effect of the two Biological Distracters respect to Non-biological Distracter. Right panel: 3D rendering of the canonical MNI template showing the localization of two regions of interest (ROI) corresponding to the left (yellow) and right (light blue) posterior parietal cortex [PPC] is reported in the axial section. Left panel: the relative plots show the mean Interference Effect [IE(inc<cong)] of the three distracters (averaged across the two effector respectively). A significant interaction was observed in these ROIs: biological distracter [G= Gaze / H= Hand] interfered on shifts of attention more than the non-biological [A= Arrow] distracter. The asterisks

indicate significant higher IE for ([G] than [A]), and higher IE for ([H] than [A]) in both regions. The level of activation is expressed in arbitrary units (a.u., ±90% confidence interval).

In other words, the BOLD signal in these regions was higher when the directional conflict between distracter-instruction signals involved biological (gaze, hand) distracters than when the conflict involved the non-biological (arrow) distracter. Confirmatory t-tests demonstrated that this effect was due to both a significant IE for gaze vs. arrow distracters and to a significant IE for hand vs. arrow distracters in left IPS and bilateral PPC. Finally, these analyses did not reveal any significant interaction for right and left FEF or right IPS, with the exception of a larger IE for [G] > [A] in bilateral FEF and a larger IE for [H] > [A] in right IPS.

Discussion

The present study had the aims to ascertain whether a possible differential attention orienting-power of directional Ingroup vs. Outgroup Gazes may relies upon commons neural substrates. Importantly, we aimed to explore whether the relationship between gaze motor effector used in the experimental task (Saccadic or Hand pointing response) was reflected in a specific modulation of the activity in the dorsal fronto-parietal nodes of the reflexive attention network.

Behavioural and neural correlates of reflexive attention

A cost of directional incongruence between distracters and instructions signals was found. All distracters in the behavioural performance showed a congruency effect both for saccadic and pointing task. This is in keeping with studies showing that attention is captured by gaze and arrows to a similar extent (Kuhn and Benson, 2007; Kuhn and Kingstone, 2009; Sato et al., 2009) and at variance from studies showing that social distracters like averted gaze or pointing hands induce stronger attentional capture more than symbolic arrow (Ricciardelli et al., 2002; Langton and Bruce, 2000). It is worth noting that in many complex daily life interactions, the tendency to follow others seems to be very strong. Thus, the lack of predominance of gaze- over arrow- distracters in triggering reflexive attention of arrows in some studies may be due to a floor effect induced by the extremely simplified reality of laboratory conditions (Kingstone, 2009; Birmingham and Kingstone, 2009). However, one may observe that the present behavioural results differed also from our previous study where gaze and hand distracters interfered more with eye and hand pointing movements respectively (Crostella et al., 2009). It should be noted however, that, differently from Crostella et al., (2009) in the current study the pointing movement was defined as a index finger extension toward the right or the left button key with the shoulder and the arm immobilized instead of a free hand arm movement in the space, accounting substantial difference in motor programming and executing.

At any rate, the present study demonstrated that, despite the instruction to focus on the imperative signal, subjects could not ignore the distracters. Importantly, the behavioural interference of directional incongruence between instruction signal and distracters was reflected in an increase of the BOLD signal. Such increase occurred in a fronto-parietal network that included the left precentral gyrus and the right middle frontal cortex bilaterally, the right supplementary motor area, the most posterior portion of the inferior frontal gyrus, the operculum, bilaterally, and the pars triangularis extending into the insula and the middle portion of the right cingulate cortex as well as posterior regions of the superior and inferior parietal cortex bilaterally. Previous studies highlighted the importance of fronto-parietal networks in a variety of attentional tasks, including covert and overt reorienting of attention to non biological stimuli (Corbetta and Shulman, 2002; Corbetta et al., 2008; Szczepanski et al., 2010), as well as to the direction of others' gaze (Grosbras et al., 2005). While studies indicate that gaze and arrows may modulate attention-shifts related activity in different brain regions (Hietanen et al., 2006) even in the absence of differences in behavioural tasks (Engell et al., 2010), only one study has thus far explored the neural network activated by mere observation of directional vs. non-directional eye gaze, hand-pointing gestures and arrows (Sato et al., 2009). This study showed activation in inferior frontal and inferior parietal areas as well as in the superior temporal sulcus common to the three distracters, even if an increase of activity in temporo-parietal clusters and in the amygdala was found for directional arrows and directional eyes respectively.

Body-part specific reference frames for mapping reflexive social attention in the fronto- parietal cortex

In keeping with previous neuroimaging studies (Grosbras et al., 2005; Hietanen et al., 2006; Sato et al., 2009; Tipper et al., 2008), our results highlight the fundamental role of fronto-parietal structures in mediating gaze and hand related shifts of attention. However, our study expands significantly previous knowledge by combining, for the first time, two main issues, namely the possible specificity of the neural representation of different effectors used for response and the influence of social and non social distracters in modulating reflexive attention. It is widely held that movements performed with different effectors are coded in different cortical regions. Distinct posterior parietal modules, for example, may preferentially code for saccades and reaches, respectively (Glimcher, 2003; Colby and Goldberg, 1999). More recent studies indicate that far from being a strict principle, effector-selectivity implies a gradual transition of preference from one effector to another, with areas of balanced activation to saccades and reaches and areas with significant preference for reaches (Levy et al., 2007). Similarly, effector preference was found in parieto-frontal areas during eye or hand movement planning but no region responded exclusively to either effector (Beurze et al., 2009). A predominance of left lateralized maps for coding the preparation of pointing movements in the presence of equivalent coding of saccadic and reaches preparation in frontal areas has also been reported (Astafiev et al., 2003). Testing the hypothesis of a difference in the visuospatial maps recruited by pointing and saccades, Hagler and colleagues (2007) identified multiple maps in both posterior parietal cortex and superior frontal cortex recruited for eye and hand movements, including maps not observed in previous studies. Although their analysis revealed subtle differences between pointing and saccades, including hemispheric asymmetries, no evidence of pointing-specific maps of visual space was found.

In the present study we explored whether biological directional distracters such as directional gaze and pointing gestures, influenced the neural underpinnings of reflexive shifts of attention in relation to the motor effectors used for the response, namely eyes or hands. To this aim, we compared the BOLD signal in the fronto-parietal ROIs that turned out to be involved in reflexive attention. We found a functional dissociation in the frontal and parietal nodes of the reflexive joint attention network, hinting at a specific influence of gaze and hand distracters in the saccadic and hand pointing tasks respectively. Overall, the fMRI data indicated that the observed interference with voluntary orienting varied as a function of central distracter-type and motor-effector. In particular, we observed greater IE-related activation in the frontal ROIs for shifts of spatial attention triggered by gaze in the saccadic task and in the parietal ROIs, specifically bilateral IPS, for shifts of attention triggered by hand in the pointing task. This result is in keeping with previous studies indicating the importance of parietal regions in mediating interference of hand movements incongruous with planning of a different hand movement (Grefkes et al, 2004) or of hand-related attention switching tasks (Rushworth et al, 2001).

Tellingly, a main point of novelty of the present study is that the fronto-parietal network subserving reflexive shifts of social attention is specially sensitive to the relationship between specific body-related distracters and the responding body parts. Importantly, an effector-specific activation of frontoparietal networks in humans has also been found in a recent study on cortical temporal dynamics of visually guided behaviour (Hinkley et al., 2010). In this study, high-gamma activity was observed in SEF and subsequently in visual cortex and FEF bilaterally, followed by a low-beta power decrease over caudal PPC during saccade execution. Thus, hand or saccadic movements implied a different functional connectivity between frontal and parietal areas.

Mirroring of attention in the fronto-parietal system

In our experimental paradigm, participants were specifically instructed to ignore the visual distracting stimuli (gaze, hand and arrow), to focus on the central imperative go signal and to maintain the fixation on the central point. Given that the distracter was presented before the unpredictable central cue, the cost of re-orienting to fully irrelevant-task distracters is likely due to interference with ongoing action programs. This may be in keeping with pre-motor theories of attention (Rizzolatti et al., 1987) and with the notion of mirroring others' actions (Rizzolatti and Sinigaglia, 2010). Behavioural studies indicate that priming a given motor response is more effective if the visual prime shares specific properties with the requested response suggesting that perceptual codes and action plans may share a common representational medium (Craighero et al., 2002). Neuroimaging studies indicate that viewing hand, mouth and foot actions may induce a specific increase of the BOLD signal in the frontal and parietal representations of the acting body parts (Buccino et al., 2001). A clear link between action mirroring and sharing of attention between individuals has been established in a single cell recording study from the monkey parietal lobe (Shepherd et al., 2009). This study demonstrates an increase of activity of parietal neurons not only when the monkey oriented his attention towards their receptive field, but also during observation of another monkey orienting in the same direction. It is also relevant that overlapping fronto-parietal cortical representations are called into play during executed, observed, and imagined reaching in humans (Filimon et al., 2007). That reflexive shifts of social attention may be coded in body-part specific coordinates and may reflect a specific tendency to imitate other movements, is indirectly suggested by a behavioural study showing that distracting gaze and hand pointing distracters impaired saccadic and pointing performance respectively (Crostella et al., 2009). The pattern of activation found in the present study likely represents neural evidence that mirroring of attention may be coded according to body-part specific reference frames.

Influence of social vs. non-social distracters on changes of BOLD signal in the fronto-parietal network underlying reflexive attention

As reported in the results section, the performance to incongruent trials was impaired with respect to congruent trials irrespectively of the distracter (gaze, pointing hand or arrow). Importantly, however, despite the equivalent interference effect of the three distracters at the behavioural level, higher changes of BOLD signal for biological (gaze and hand-pointing) than non biological distracters were found in the bilateral PPC and left IPS regions. This suggests that hemodynamic brain responses may be more sensitive than behavioural responses in signalling selective influences on attentional shifts and thus in highlighting the special contribution of the parietal-frontal network to reflexive social attention (Deaner and Platt, 2003). Thus biological stimuli, possibly because of their social relevance, may have an inherently higher power in catching attention than non-biological stimuli even when this is not elected in the behavioural performance. This result is in keeping with a recent fMRI study showing that even though the interference of gaze and arrows was comparable at the behavioural level, only the latter distracter modulated neural activity in the temporo-parietal attention network, thus indicating that different neural substrates underpin reflexive attention mediated by biological and non-biological cues (Engell et al., 2010).

Conclusion

Our study indicates that frontal and parietal cortical regions map the conflict between a central cue instructing leftward or rightward saccadic or hand pointing movements directions and to-be-ignored distracters (gaze, hand and arrow) pointing in opposite direction. Crucially, however, the detrimental effect of the directional conflict induced by gaze and hand distracters brought about differential activation in parietal and frontal structures depending on whether subjects performed a saccadic or hand-pointing task. In particular, the distracting effect of pointing gestures is associated with higher parietal activity when the motor task is performed with the hand. By contrast, the distracting effect of averted gaze is associated with high frontal activity when the motor task is performed with the eyes. It is worth noting that the distracting effect of arrows induced increased activity in the fronto-parietal network independently from the effector used for the response but overall to lesser degree than biological distracter. This pattern of results indicates, for the first time, that reflexive social attention is coded in the fronto-parietal cortex according to body-part centred coordinate systems.

Chapter 6

"Politics in your eyes": Behavioral and Neural evidences of Reflexive Social Attention modulated by Political Affiliation

An interesting study published by Shepherd and collaborators (2006) demonstrated that "Social Status" gates social attention in low- and high- status monkeys. By probing the impact of social status on gaze-following in rhesus macaques performing a simple visual orienting task, the results confirmed prior reports that gaze-following in nonhuman primates, as in humans, is composed of reflexive and voluntary components (Tomasello et al., 2001; Friesen et al., 2004). The fact that the strength of these mechanisms varies with social status may allow to speculate that variation in reflexive and voluntary gaze-following among monkeys may share features with variation in social attention in humans. For example, the balance between reflexive and voluntary social attention may be set by neuromodulatory systems associated with differences in personality or temperament (Claarke and Boinski, 1995; Bercovitch and Ziegler, 2002).

No human studies have so far addressed the issue of the variables that can influence the relationship between the individual who provides the interfering gaze and the individual who is influenced by the gaze. Political psychology studies indicate that choice behaviors, such as voting preferences, are strongly influenced by how the candidate is perceived and by the voters' specific personality traits (such as for example the perceived similarity with political leaders) (Caprara and Zimbardo, 2004). These series of experiments will test the hypothesis that the social status attributed to the individual influences his capability to orient the gaze of an observer. We applied the gaze-cuing paradigm (only saccadic task used in the first fMRI experiment) to individuals with known political preferences and set of values that influence voting behaviour (Caprara et al., 2007). In both experiments, the distracting gaze belonged to political leaders or opinion-makers of the same or opposite coalition with respect to the experimental subjects. We hypothesized that the attentional catching effect of gaze was stronger when the similarity between the observed model and the observing individual was high (e.g. when the experimental subject report a strong tendency to identify himself with the model). We anticipated that the onlooker may follow the direction shown by the gaze of his/her favourite political leader based on the inference that the indicated direction may signal a potential danger or a source of reward. These studies allowed us to explore whether the automatic behaviour underlying reflexive joint attention mechanism can be implicitly modulated by the social status of the gazing individual and by the onlookers' personality.

In the next sections, first I will present results obtained on a behavioral experiment realized by tracking saccadic movement during a gaze-cuing task and second, using the same paradigm (but different distracting face and experimental subjects) some "preliminary conclusions" about BOLD responses underlying the interference effect of in-group politicians and opinion-makers in voters belonging to the same or different political affiliation.

Experiment 2

As mentioned before, a recent study on monkeys (Shepherd et al, 2006) showed that low-status male rhesus macaques reflexively follow the gaze of all familiar rhesus macaques, but high-status macaques selectively follow the gaze only of other high-status monkeys. In this study we wanted to test if a similar modulation can be assessed in humans, whereas, at least in Western Countries, have organized their societies in democracies in which at least two groups compete to take the power. Choosing a party or a political group generically gives us a social identity (Tajfel and Turner, 1979). Affiliation allows us to rapidly categorize individuals between in- and out-group. This act of categorization may be made consciously or unconsciously (Perdue et al., 1990). In this study, we anticipated that political affiliation can affect the automatic process of reflexive social attention. To explore this possibility, we first divided 27 participants in two groups, left-wing (N=14) and right-wing (N=13), on the basis of a questionnaire in which they reported their political orientation and their voting behaviour. During the behavioural task, participants were asked to perform a left or right-ward saccadic movement towards two lateral targets according to the colour changing of an imperative-cue. During the task, a face appeared and performed a gaze congruent or incongruent with the direction cued by the imperative signal. Congruent and incongruent distracting gaze were equiprobable and occurred 75 ms before the imperative cue, in order to optimize the interference with the task (Ricciardelli et al., 2002). Distracting faces portrayed well-known actual or former political leaders and opinion-makers: Silvio Berlusconi (an actual political leader), Bruno Vespa (an opinion-maker), Antonio Di Pietro (an actual political leader) and Romano Prodi (a former political leader). Before the saccadic task, each distracting gaze was judged by subjects as belonging to two democratic and liberal political party (i.e. Berlusconi and Vespa were considered centre-right wing, Prodi and Di Pietro centre-left wing). We hypothesized that if reflexive social attention would be modulated by the political affiliation of the observer, then a higher gaze-following effect should be enhanced when they had to perform the incongruent saccadic movement respect to that one indicated by the member of their own political party. Furthermore, we investigated the role of personality dispositions in reflexive social attention. Numerous studies have underlined the relation between the personality characteristics of voters and their political affiliation. Among them Caprara and Zimbardo (2004) offered a conceptual framework that highlights the congruencies between voters' traits, programs of favoured political coalitions, and personalities of political leaders. In accordance with the "Congruency Model", we hypothesized that perceived similarity would be correlated with the modulation of reflexive social attention according to different political affiliation of voters. In particular, we predicted that the more people perceive their own personality as similar to the personality of the distracters, the more they would follow their gaze. In order to assess this hypothesis, subjects described themselves using a list of 25 adjectives and provided their perceptions of Berlusconi, Prodi, Vespa and Di Pietro using the same list and we computed a perceived similarity index.

Following previous researchers (Crostella et al., 2009), we used participants accuracy in performing the task as a dependent variable. A Gaze Following Index (GFI) was deducted by subtracting the incongruent trials minus the congruent trials for each observed-face. Thus, GFIs were entered in a 2x4 mixed model ANOVA with the subject group (centre-left, centre-right) as between-subject factor and the four observed-faces (Berlusconi, Di Pietro, Prodi, Vespa) as within-subjects factor. In accordance with our hypothesis, ANOVA showed a significant interaction between Distractor and Group (F(3,75)=6,87, p = .002, η^2_p = .18). In fact, right-wing participants scored higher GFIs when attending to in-group distractors than their out-group: with Berlusconi (mean: 18.4% GFI) more than Di Pietro (mean: 8.5% GFI, p = .02) and Prodi (mean: 4.1% GFI, p < .01); with Vespa (mean: 17.2% GFI) more than Di Pietro (p < .05) and Prodi (p < .01); GFIs with Berlusconi and Vespa didn't differ each other (p = .77), neither with Prodi and Di Pietro did (p = .13). On the other side, within centre-left group, the post-hoc showed a trend (p = .14) leading to a difference between Berlusconi and Di Pietro, showing Di Pietro followed more than Berlusconi (mean: 8.9% GFI vs. 2.1%). Our hypothesis on the relation between congruency model (Caprara and Zimbardo, 2004) and gaze-following behaviour strength was confirmed by a significant positive correlation between perceived similarity and GFI with Berlusconi as distracter (r = .50, p < .01). Positive correlations were found also with Prodi (r = .27, p = .18) and Di Pietro (r = .27 p = .18) although they fail to reach statistical significance. Consistently with our hypothesis, we found that reflexive social attention is influenced by complex higher-order cognitive and social dimensions as politic affiliation and personality dimensions. In particular we found that within the right-wing group, this attention-catching power was revealed to be stronger when distracters political affiliation was coherent (i.e. Berlusconi and Vespa). Within left-wing group, on the other hand, we failed to find such significant difference, even if there's was a difference in trend between Di Pietro and Berlusconi that shows that left-wing onlookers tend to follow more their leader's Gaze than the gaze of the opponent coalition leader. Anyway, the difference we found within the left-wing group is not only less significant but clearly less strong than the effect we found in the right-wing group. This asymmetry could be due to a difference between stimuli: while Silvio Berlusconi is currently the leader of the centre-right coalition, during the period in which we ran the experiment, centre-left coalition did not have a stable leader because they were in a transitory political situation, so we chose the leader of a minor centre-left party. Another possible explanation could deal with personality differences in authority acceptance between the two groups. Right-Wing Authoritarianism (RWA), indeed, is a strong predictor of political orientation (Dukitt, 2001; Feldman, 2003) and people who scored high in RWA scale are likely to accept more a strong leadership and tend to conform more to the others. This may explain the reason why right-wing voters tended to follow their leader, in an implicit and automatic way.

As hypothesized, perceived similarity played a role in this effect. In fact, the more the voters perceived themselves as similar to Berlusconi, the more they were likeable to follow his gaze. The fact that the correlation between GFI and perceived similarity scores with Di Pietro and Prodi did not reach significance probably is due to the fact that Berlusconi showed a personality that matched with the voters belonging to their political party. It is important to stress that our results are not explainable by other variables such as media exposure or influence, because distracters ratings on these dimensions failed to correlate with the relative GFI scores.

To conclude, this study suggests that reflexive social attention mechanism is not subserved by a specific module, impermeable to contextual cues, as we demonstrated that political affiliation, that needs a complex social knowledge can penetrate the neural circuits controlling gaze cuing. This finding is very challenging because this modulation is driven by information that is not immediately available from the visual features of the distractor, but relies on a cognitive and affective complex dimension, i.e. political affiliation. Political affiliation has already demonstrated to play an important role in categorize very rapidly individuals as in-group vs. out-group members in an automatic manner (unconsciously and rapidly). It seems that this dimension plays an important role in our live. Not surprisingly, if we consider that humans have been evolved in large-scale societies in order to manage cooperation behavior, political groups and collective political behaviors as voting in elections (Fowler and Schreiber, 2008) could be considerate a prerogative of human society. Within this framework, our data suggest that we tend to follow the gaze of an in-group more than out-group member, with whom we share ideology (Jost, Federico and Napier, 2009), but also stable values and personality traits. According to our results, this process seems to be stronger in right-wing groups, but we are not able to explain it definitively in a unique way, probably because of a dispositional difference toward authority and conformism, as right-wing political orientation correlate with a scale that measure these ideological dispositions (Altemeyer, 1988).

Finally, we found that politicians whose personality hold a better match with that of voters are not only more likeability to be voted (Caprara et al., 2007), but also exert a powerful attentional capture on voters.

Method

Participants

Thirty-six subjects took part in the study. All had normal or corrected to normal vision with no history of neurological or psychiatric disease and were naïve to the purposes of the study. Because of errors in eye movement data collection, three subjects were excluded from analysis. We further excluded five participants (15%), from whom less than 50% of trials were recorded. This left 28 subjects (12 males, mean age = 25.25; SD = 2.89). After having received an explanation of the procedures, they provided their written informed consent to participate in the study. The study was approved by the independent Ethics Committee of the Santa Lucia Foundation (Scientific Institute for Research Hospitalization and Health Care). Data were recorded among 24th of July, 2009 and 24th October, 2009.

Stimuli and Procedures

Measures

Participants were administered a self-reported questionnaire in order to collect: a) socio-demographic variables such as gender, age, and education level; b) concern in politics; participants were asked their degree of interest in politics, from 1 (not at all interested) to 5 (highly interested), and the frequency with which they discuss politics with their family members, colleagues at work, acquaintances, and friends, from 1 (never) to 5 (every day); c) political orientation, participants were asked to place themselves on seven Likert type scale ,where 1 is "extreme left wing", and 7 is "extreme right wing"; d) voting behaviour, participants were asked for which party they voted in the last European political elections (June, 2009). For each Likert scale we presented a photography of each distractor face. Under each photography, participants had to answer in a 1 to 5 Likert scale in order to rate:

a) *Exposure*: "please rate how much do you know, through the media, and about issues linked to his role, the personality x" where 1 is "I know him very well" and 5 is "I don't know him at all".
b) *Influence*: "please rate how much do you think x is influent within the Italian political landscape" where 1 is "very influent" and 5 is "not influent at all".

Finally, subjects had to rate which is the political orientation of the distractor, considering his ideas, in a 1 to 7 scale, where 1 is extreme left wing, and 7 is extreme right wing. Furthermore, subjects had to answer to the item of the following tests, presented in a computer monitor by Cogent2000 software (www.vislab.ucl.ac.uk/Cogent/). The presentation of the scales was randomized between subjects.

Right-wing authoritarianism scale: The participants completed an Italian version of Altemeyer's Right-Wing Authoritarianism Scale. The scale includes 30 statements on a seven-point Likert type scale ranging from 1 ("strongly disagree") to 7 ("strongly agree"). To reduce response set, half of the items were negatively worded (e.g. "The 'old-fashioned ways' and the 'old-fashioned values' still show the best way to live") and half were positively worded (e.g. "You have to admire those who challenged the law and the majority's view by protesting for women's abortion rights, for animal rights, or to abolish school prayer"). Items were coded so that a high score indicated high authoritarianism. Cronbach's alpha for the present study was .96 (see Supplemental Materials).

Personality measures: Participants rated themselves on the Five Factors of personality described themselves using a list of 25 adjectives and provided their perceptions of Berlusconi, Prodi, Vespa and Di Pietro using the same list. The list included five markers each of: Energy/Extraversion (happy, determined, dynamic, energetic, active); Agreeableness (cordial, generous, loyal, sincere, unselfish); Conscientiousness (efficient, scrupulous, precise, conscientious, diligent); Emotional stability (optimistic, self-confident, solid, relaxed, calm); and Intellect/Openness to experience (sharp, creative, innovative, modern, informed). The adjectives were selected from a larger list of adjectives that have previously been identified in the Italian lexicon as being among the most frequently used to describe human personality and also the most representative of each of the dimensions of the Big Five (Caprara and Perugini, 1994). Each adjective was rated for how characteristic it was of each target on a 1 (“not at all”) to 5 (“very much so”) scale. To measure similarity, an index was created that represented the similarity between the self and each of the four personalities. First, perceived dissimilarity was computed for each adjective by using the generalized Euclidean distance measure, (*d*) between the personality ratings of the self and the four politicians in question. Dissimilarity was calculated at an overall level, averaging scores across all 25 adjectives. These scores were transformed into a range from 0 to 1 by using the following equation: ∂ = d/dmax, where ∂ is the normalized index and d is the raw index. Finally, we subtracted from 1 by converting the distance or dissimilarity scores into similarity scores, ranging from 0 (not similar at all) to 1 (completely similar) (See Supplemental Materials).

Additional Results

The two groups didn’t differ for age (p=.47) nor education (p=.42) nor interest in politics (p=.54). We didn’t find any correlation between GFI and models reported influence or mediatic exposure (*ps*>.05). Emotions toward Berlusconi (computed as positive emotions minus negative emotions) correlated positively with Berlusconi’s GFI (r=.44; *p*=.03), but it seems to be a side effect of the political affiliation. In fact, a significant interaction between the reported model orientation and the group occurred (F(3,72)=19.96, *p*<.00001). Duncan post-hoc comparison confirmed that right- and left-wing participants showed an emotional in-group bias toward all of the models (*ps*<.01) but Di Pietro (albeit the difference showed a trend toward significance (p=.06)).

Eye movement recording

The study was performed in a quiet room with medium illumination (about 64 cd/m2). Subjects sat on a comfortable chair in front of an LCD monitor, positioned at about 57 cm from their eyes. Eye position and eye movements were measured monocularly in real-time by means of an infrared video-based system (ASL 504 Remote Tracker, Applied Science Laboratories, USA). The experiment was created and ran with E-Prime software (version 1.1, Psychology Software Tools, Inc., Pittsburgh, PA) on an IBM compatible computer. Saccadic eye movements were collected via a blocked protocol in a 2x4 factorial design. In each block, stimuli comprised the factorial combination of the two *Condition* respect to the imperative cue (congruent and incongruent), and the four types of *Observed-faces* (Berlusconi / Prodi / Vespa/ Di Pietro). These factors were manipulated among the two types of political orientation of participants (left or right-wing political orientation). Each trial started with the appearance of a black central fixation mark (0.21° x 0.21° in size) presented on a light gray (about 47 cd/m2) background, and of two black squares (0.43° x 0.43°) presented at 10.2° of eccentricity in the left and the right visual field. After 575 msec, the color of the central mark changed to either blue or orange. This was the imperative signal for making a fast and accurate saccade toward the left (change into blue) or the right (change into orange) target square. The coloured cue remained visible until the end of the trial. A distractor's gaze was presented behind the central fixation mark, at intervals of 75 ms from the onset of the instruction-cue (stimulus onset asynchrony, SOA) because we demonstrated that gaze following specifically occurs at this interval (Crostella et al., 2009; Cazzato et a., 2010). The gaze could belong to one of these personalities linked to the world of Politics: a) Silvio Berlusconi; b) Antonio Di Pietro; c) Romano Prodi; d) Bruno Vespa. While a) and d) were considered to be center-right wing (their means were respectively 5.6 and 4.7 both of them significantly over the 4, *ts* more than 2.9, *ps*<.01), b) and c) are considerate to be centre-left wing (respectively 3.1 and 3.0, both of them significantly below 4, *ts*=less than -3.9, *ps*<.001). Distractor a) and distractor b) are actually involved in politics, being a) the actual Prime Minister and the leader of the centre-right coalition and b) one of the most visible leaders of the centre-left coalition). Instead, distractor c) is a former center-left coalition leader, but is not involved in politics anymore, and distractor d) is an opinion-maker journalist, well known among the general public as a sympathizer of the center-right political coalition, actually in power. For each observed-face we prepared a RGB digital photography (6.76° x 6.76°). To enhance their saliency, the stimuli were animated by two frames presented in rapid sequence. The first frame (lasting 500 ms) was replaced by a second frame lasting 600 ms. The first frame depicted a straight gaze. The second frame depicted a gaze which could be oriented leftward or rightward (as shown in figure 1 of the main text). The direction of the distractor and that one indicated by the instruction-cue could be congruent (C) (for instance: both leftward) or incongruent (for instance: one leftward and the other rightward).

Note that subjects were instructed to ignore the distracting stimulus and to focus their attention on the central mark colour change. Subjects were tested in four separate blocks, each associated with one type of observed-face. In each block, the two instruction cues (leftward or rightward) and the two distractors (congruent or incongruent) were equally probable and were presented in a random sequence. Each of the 4 possible combinations was repeated 12 times, for a total of 48 trials per block. We analyzed subjects' directional accuracy by focusing on the first horizontal saccade that followed the instruction cue and had an amplitude larger than 2°. Saccadic RTs were also collected. Only RTs for correct trials were considered. Trials in which signal was dirty were excluded (725 out of 5376, 13,5%). Trials were rejected from the analysis described below if the latency was either less than 100 ms (anticipations) or greater than 500 ms (delays). The proportion of rejected trials was 3,4% of the total trials.

Experiment 3

The first experiment aimed at investigate whether reflexive social attention is permeable to high-order social variables such as political affiliation and the perception to be similar to an ingroup political representative. To explore this issue we used a social attention paradigm in which the directional gaze of right- or left-wing Italian politicians or opinion-makers could influence the oculomotor behaviour of ingroup or outgroup voters. The results showed a strong interference effect of Right-wing leader (Berlusconi), being right-wing voters prone to follow more their ingroup leader than the outgroup leader. The effect was not clearly evident in left-wing group, seen that the attentional capture effect did not approach the significance for the ingroup faces. We can speculate that these results seem to reflect the current political equilibrium, indicating that complex social variables penetrate and influence automatic shifts of attention.

On the basis of our results, we performed an fMRI study with the idea to explore brain responses underlying the gaze following effect (i.e. interference effect) of in-group politicians and opinion-makers in voters belonging to the same or different political affiliation. First, we anticipate that covert and reflexive components of the fronto-parietal attentional network should be involved in the oculomotor execution by signalling the incongruence between observed-gaze and direction of saccade to be performed of an onlooker. This signalling or reorienting to salient stimuli should be called into action when similarity between voters and ingroup political members is high. In addition, we expected to highlight the involvement of subcortical areas, linked to emotional and “metalizing” components, as well to frontal and parietal nodes well known to be involved in gaze-cuing task.

Experimental Procedure

Subjects

We recruited volunteers by placing flyers at public places and university campus (Città Universitaria at “Sapienza” University of Rome); posting information on internet political discussion group and in a virtual social network. Recruitment materials requested right-handed men and women, ages 18-36 years, who were supporting right- or left-centred wing coalition and were informed about main principal political events and the actual Italian political situation. We carried out all the screening and scanning sessions from late December 2009 until early April 2010, close to the local elections (March the 28th-29th on 2010). Potential subjects were screened by phone using a magnetic resonance imaging questionnaire (to rule out safety risks, neurological disorder and eyeglasses) and a political attitudes questionnaire using general questions to evaluate interest in politics and political orientation. We included subjects evaluating themselves as strong right- or left-wing politically orientated. In addition after scanning session, participants were asked to fill in several Likert scales assessing the interest and attitude toward politics. A rating for each face about political orientation, influence, exposure and emotional valence as well as answer to questionnaire on their personality

(See Stimuli and Procedures section) was requested to them. A total of thirty healthy participants were scanned (male: 19; mean age: 23.11 years, range: 19-29, female: 11; mean age: 23.73 years, range: 18-27). The reported analysis were based on 28 normal subject (14 right-wing: male, N= 8; female, N= 6; 14 left-wing people: male, N= 10; female, N= 4), therefore two subjects were excluded because of technical problems during data acquisition. All were Italian citizens, right-handed and native Italian speakers. All subjects had normal or contact-corrected-to-normal visual acuity. After having received an explanation of the procedures, participants gave their written consent. The study was approved by the independent Ethics Committee of the Santa Lucia Foundation (Scientific Institute for Research Hospitalization and Health Care).

Stimuli and Procedure

Self-report measures

1) Likert Scales

After scanning session, participants were administered a self-reported questionnaire in order to collect their degree of interest in politics, from 1 (not at all interested) to 5 (highly interested), and the frequency with which they discuss about politics with their family members, colleagues at work, acquaintances, and friends, from 1 (never) to 5 (every day). In addition, with the aim to be sure about their political orientation, participants were asked to: a) place themselves on seven Likert type scale, where 1 is extreme left-wing, and 7 is extreme right-wing; b) express their voting behaviour, namely in the last National political elections (April, 2008), the European political elections (June, 2009) and the intention to vote in the future local political elections (March, 2010). These measures allowed us to control that participants political attitude was coherent and strong with respect to their voting preference about past and future political coalition. None of the subjects that declared to vote for the right- or left-wing coalition had ever voted for the opponent party in the past. For each Likert scale we presented a photograph of each distracting face. Under each photograph, participants had to answer in a 1 to 5 Likert scale in order to rate (See Supplemental Materials):

a) *Exposure*: “please rate how much do you know, through the media, and about issues linked to his role, the personality x where 1 is “I know him very well” and 5 is “I don’t know him at all”;
b) *Influence*: “please rate how much do you think x is influent within the Italian political scenario” where 1 is “very influent” and 5 is “not influent at all”;
c) *Emotional valence*: is an overall score computed for each face by subtracting negative emotion scores by the positive ones; we asked to participants: “please rate how much do you think x arouses positive emotions” where 1 is “not positive at all” and 5 is “very positive” and “please rate how much do you think x arouses negative emotions” where 1 is “not negative at all” and 5 is “very negative”. Negative values indicated a negative emotional valence while positive values indicated a positive emotional evaluation of each Observed-face.

Most importantly, subjects had to rate which is the political orientation of the distracter, considering his ideas, in a 1 to 7 scale, where 1 is "extreme left wing", and 7 is "extreme right wing". These rating allowed us to categorize the four characters accordingly to the participants' point of view. No subjects rated as left-wing politically oriented Berlusconi or Vespa, nor Bersani or Floris were judged as belonging to right-wing coalition. Finally, subjects had to answer to the item of the following tests, presented in a computer monitor by Cogent2000 software (www.vislab.ucl.ac.uk/Cogent/). The presentation of the scales was randomized between subjects.

2) *Personality traits and Similarity Score*

As in Experiment 2, participants described themselves using a list of 25 adjectives and provided their perceptions of Berlusconi, Bersani, Vespa and Floris using the same list. The list included five markers each of: Energy/Extraversion (happy, determined, dynamic, energetic, active); Agreeableness (cordial, generous, loyal, sincere, unselfish); Conscientiousness (efficient, scrupulous, precise, conscientious, diligent); Emotional stability (optimistic, self-confident, solid, relaxed, calm); and Intellect/Openness to experience (sharp, creative, innovative, modern, informed). The adjectives were selected from a larger list of adjectives that have previously been identified in the Italian lexicon as being among the most frequently used to describe human personality and also the most representative of each of the dimensions of the Big Five (Caprara & Perugini, 1994). Each adjective was rated for how characteristic it was of each target on a 1 (not at all) to 5 (very much so) scale. To measure similarity, an index was created that represented the similarity between the self and each of the four personalities. First, perceived dissimilarity was computed for each adjective by using the generalized Euclidean distance measure, (*d*, Cronbach & Gleser, 1953) between the personality ratings of the self and the four politicians in question. Dissimilarity were calculated at an overall level, averaging scores across all 25 adjectives. These scores were transformed into a range from 0 to 1 by using the following equation: $\delta = d/dmax$, where δ is the normalized index and d is the raw index. Finally, we subtracted δ from 1 by converting the distance or dissimilarity scores into similarity scores, ranging from 0 (not similar at all) to 1 (completely similar).

Experimental Paradigm: Gaze-cuing task

Participants were positioned in the scanner, in a dimly lit environment. The experimental visual stimuli were presented via a mirror mounted on the MRI headcoil (total display size 19.5° x 14.6° degrees of visual angle, 1.024 × 768 screen resolution, 60 Hz refresh rate). The visual stimuli were back-projected on a screen behind the magnet. Stimulus presentation was controlled with Cogent2000 (www.vislab.ucl.ac.uk/Cogent/). Each trial started with the appearance of a black central fixation mark (0.5° x 0.5° in size), presented centrally against a grey background**,** and of two black squares (1.4° x 1.4° in size), presented for 500 ms at 7.5° of eccentricity in the left and the right visual field. Twelve digital pictures, three for each face, were gathered from the news media in internet. The distracting gaze consisted of digital modified photographs of the face of well-known Italian right- or left-wing political leaders (Silvio Berlusconi, Pier Luigi Bersani) or right- or left-wing perceived opinion-makers (Bruno Vespa, Giovanni Floris). It is important to note that, while Silvio Berlusconi is the actual Prime Minister and the leader of the centre-right coalition and Pier Luigi Bersani is the leader of the centre-left coalition, Bruno Vespa and Giovanni Floris are both opinion-maker journalists, and were categorized by our participants as sympathizers of the right and left-wing political coalition respectively (See Results section). The choice of each photo was determined on the basis of the following criteria: a) the individual had no facial hair; b) the individual was facing the camera; c) the individual had a neutral or smiling expression (to control for emotional content, we chose for each character two neutral and one smiling photo); d) the image had an acceptable resolution; e) the photo was taken under normal conditions. For each face, the irises and pupils of the eyes were cut from the original photographs and pasted to fit on the right or left side of the eyes using Photoshop 8.0.1 (Adobe, CA). To obtain a striking attentional-capture effect, the stimuli were animated by presenting two frames in rapid sequence. The first frame depicted a straight gaze, while the second frame, which depicted a left- or rightward oriented gaze, replaced the first frame. The direction of the distracting face and the one indicated by the instruction-cue could be 50% of the time congruent or incongruent. Before starting the fMRI acquisition each participant was asked to perform outside the scanner a training task in which they had to learn with 100% accuracy on 48 consecutive trials, the association between instruction signal (red or blue) with leftward or rightward saccadic movements. In the scanner, each trial started with the presentation behind the black fixation mark of a straight gaze which lasted 500 ms. At 500 ms, a second frame, that depicted left- or rightward oriented gaze, replaced the first frame and created a strong animation effect. The directional distracters remained on until the end of the trial. 75 ms after the oriented distracter presentation, the black central fixation mark (imperative-cue) changed to either blue or red colour (Ricciardelli et al., 2002; Crostella et al., 2010; Cazzato et al., 2010). This was the instruction signal for the subjects to make a saccade movement towards the left (change into red) or the right (change into blue) target square. Thus, the direction of the distracter and that indicated by the instruction-cue could be congruent (left-red or right-blue) or incongruent (left-blue or right-red). The face remained visible until the end of the trial. In order to engage automatic processes and minimize expectations, the directional gazes were equiprobable (50% congruent) and non-predictive. It is worth noting that the subjects were instructed to ignore the distracting gaze and to focus on the central mark colour change. Moreover, they were explicitly informed that the instruction cue was not informative on the direction of the distracters. In order to avoid subjects anticipating stimuli, a random inter-trial interval ranging from 3.5 to 4.5 s was used (See Figure 1).

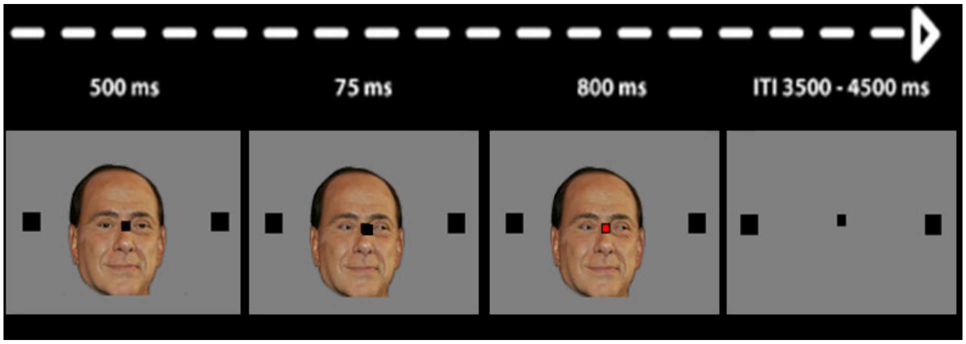


Figure 1: Trial event with a possible distracting face (incongruent condition). At the beginning of the trial, a straight gaze was presented behind a black fixation mark (500 ms). Turning the black fixation point into red was the imperative instruction signal for leftward saccades. Only incongruent condition is represented for the sake of simplicity.

Eight event types were organized in a 4 x 2 factorial design. One factor was the type of *Observed-faces*: Berlusconi-Bersani-Vespa-Floris. The second factor was the *Congruence*: congruent vs. incongruent direction between instruction signal and observed-face. Congruent and incongruent directional combinations of instruction cues and distracters were presented in unpredictable and randomized order. These factors were manipulated among the type of *Political Affiliation* supported by the participants (left- or right-wing political orientation). Thus, fMRI data were acquired via a mixed, blocked (Observed-faces)/event related (Congruence) protocol. All participants underwent five fMRI runs. Each participant completed a total of 720 trials, therefore each imaging session consisted of 36 repetitions for each of the four observed-face (Berlusconi-Bersani-Vespa-Floris), respectively 18 for congruent and 18 for incongruent conditions (balanced for left/right direction and red-blue imperative-cues). Each scanning session lasted approx. 10 min for a total experiment duration of about 50 min.

Eye movements recording

In the training session outside the scanner, subjects sat in front of a computer screen. In all subjects, eye position and saccadic movements were monocularly monitored using an infrared video camera (Sony EVI D31, color video camera, Sony JP). Participants were instructed to look at the location indicated by the instruction-cue and then to quickly look back at the fixation point. During the scanning session, again the participants' saccadic movements were monocularly monitored in real-time by means of an ASL eye-tracking system that was adapted for use in the scanner (Applied Science Laboratories, Bedford, MA; Model 504, sampling rate: 60 Hz). For each subject the eye-tracking system was calibrated before fMRI scanning. The calibration was repeated during the experiment whenever necessary. Eye-position traces were examined in a 2500 ms time window, beginning with the imperative cue onset until the end of the trial. Saccadic RTs were calculated from the target onset time to when an horizontal eye position exceeded 2°. Mean saccadic RTs and accuracy were calculated collapsing left and right directional target trials. We did not compute those saccadic movements performed following distracting gaze instead than instruction cues (incorrect responses), misses (no response), anticipations (RTs < 100 ms) and retards (RTs > 800 ms).

Image Acquisition and Analysis

A Siemens Allegra (Siemens Medical Systems, Erlangen, Germany) operating at 3T and equipped for echo-planar imaging (EPI) acquired functional magnetic resonance (MR) images. A quadrature volume head coil was used for radio frequency transmission and reception. Head movements were minimized by mild restraint and cushioning. Thirty-six slices of functional MR images were acquired using blood oxygenation level-dependent imaging (3.0 x 3.0 x 2.5 mm thick, 50% distance factor, TR = 2.34 s, TE = 30 ms), covering the entire cortex. We used the statistical parametric mapping package SPM5 (www.fil.ion.ucl.ac.uk) implemented in MATLAB (v 7.1, The MathWorks, Natick, MA) for data pre-processing and statistical analyses. For all participants, we acquired 1.275 fMRI volumes, 255 for each run. The first four image volumes of each run were used for stabilizing longitudinal magnetization and were discarded from the analysis. Pre-processing included rigid-body transformation (realignment) and slice timing to correct for head movement and slice acquisition delay. Residual effects of head motion were corrected for by including the six estimated motion parameters for each subject as regressors of no interest. Slice-acquisition delays were corrected using the middle slice as a reference. All images were normalized to the standard SPM5 EPI template, resampled to 2 mm isotropic voxel size, and spatially smoothed using an isotropic Gaussian kernel of 8 mm FWHM. Statistical inference was based on a random effects approach (Penny and Holmes, 2004). First, for each participant, the data were best-fitted at every voxel using a combination of effects of interest. These were delta functions representing the onsets of the 8 conditions given by the crossing of our 4 x 2 factorial design: *Observed-face* [Berlusconi / Bersani / Vespa / Floris] x *Congruence* [congruent / incongruent] convolved with the SPM5 hemodynamic response function. The onset of the hemodynamic response function was aligned with the onset of the imperative cue with duration = 0. Onsets of trials in which an erroneous response or an eye movement toward the wrong side occurred were included in the design matrix as covariates of no interest, but excluded from any further analysis. With the aim to investigate whether the reflexive joint attention mechanism is modulated by the interaction between *Observed-face* and P*olitical Affiliation* "with and without" taking into account the *Congruence* factor, two main fMRI analysis were performed:

1) In the first analysis, linear contrasts were used to determine differential brain responses for incongruent minus congruent conditions (IE = Incongruence Effect) separately for the 4 Observed-faces (e.g. [Berlusconi (Incong) > Berlusconi (Cong)]).

2) In the second analysis, again for each Observed-face, linear contrasts were used to determine the mean effect of congruent and incongruent condition (FO = Face Observation effect) (e.g. [Berlusconi (Incong) + Berlusconi (Cong)], both analysis averaging the 5 fMRI runs.

Four contrasts images were entered in a 4×2 factorial ANOVA with *Observed-face* [Berlusconi / Bersani / Vespa / Floris] and type of *Political Affiliation* supported by participants [Right- / Left-wing] separately for each analysis. Finally, linear contrasts were used to compare the IE or the FO, using between-participants variance (rather than between scans). Correction for nonsphericity

(Friston et al., 2002) was used to account for possible differences in error variance across conditions and non-independent error terms for the repeated measures. Both analysis aimed at determining: a) the brain regions called into action when directional cue and the observed-faces provided conflicting directional information (only for IE analysis); and irrespective of Political Affiliation of voters, whether reflexive joint attention was differentially modulated by: b) the Social Role of each Observed-face [Political Leader > Opinion-Maker]; c) the Political Coalition of each Observed-face [e.g. (Right-wing faces) > (Left-wing Faces)]. Finally, respectively to the Political Affiliation of participants, d) whether any modulation is exerted by Ingroup's Observed-face [e.g. (Right-wing Group (Berlusconi + Vespa)) > (Left-wing Group (Bersani + Floris))]; e) if reflexive joint attention resulted modulated by the social membership of Ingroup Political Leader with respect to Opinion-maker [e.g. (Right-wing Group (Berlusconi > Vespa))].

Results

Demographics

Given that the gaze-cuing paradigm required the subject has a strong preference for a certain political coalition, we asked to participants to express their preference on a scale from 1 "strongly left-wing" to 8 "strongly right-wing", including the "apolitical" condition to assess our critical manipulation. None declared to be "apolitical", therefore no subject of our sample was excluded for this reason. Therefore, we obtain a final sample of two right-wing and left-wing participants groups of 14 subjects respectively. No significant differences in age [t(1,26) = .241, n.s.], nor in years of education [t(1,26) = -.192, n.s.] were found between the two group. With regard to interest in politics, a significant difference was found between group, given that left-wing participants declared to be more interested [t(1,26) = -3.280, p =.003] and informed about politics [t(1,26) = -2.362, p = .026] with respect to right-wing participants.

Self-report measures

Each Likert scale about *Exposure*, *Influence* and *Emotional valence* was investigated by means of a repeated-measures of variance with Observed-face (4 levels: Berlusconi/Vespa/Bersani/Floris) as within-participant factor and Group (right- or left-wing voters) as between-group factor. Planned comparison were Bonferroni corrected. We displayed these results in Figure 2 A-B.

Ratings of Familiarity, Political Influence and Emotional Valence for In- and Out-group Character.

A significant main effect of political orientation of observed-face [F(3,26) = 17.802, p < .001] was found. Planned comparisons revealed that Berlusconi was the most familiar character, while Vespa significantly differed with respect to Berlusconi and Bersani. Bersani instead was less familiar than right-wing character and did not differ from Floris. Finally left-wing opinion-maker Floris only significantly differed from Berlusconi. The interaction between exposure of each observed-face and Group [F(3,26) = 3.008, p < .05] revealed that right-wing participants rated as familiar right-ingroup faces more than left-wing outgroup faces. Not surprisingly, left-wing participants rated as familiar left-wing ingroup faces less than outgroup right-wing faces, being Berlusconi the most familiar also for the left-wing group. (See Figure 2 A). As illustrated in Figure 2 B, a main effect of observed-face was found when we asked to participants to rate how much do they think each character is influent within the Italian political landscape [F(3,26) = 27.943, p < .001]. Both group reported that Berlusconi was the most influent with respect to the other observed-faces. Finally, no interaction between observed-face and Group was observed [F(3,26) = .766, n.s.].

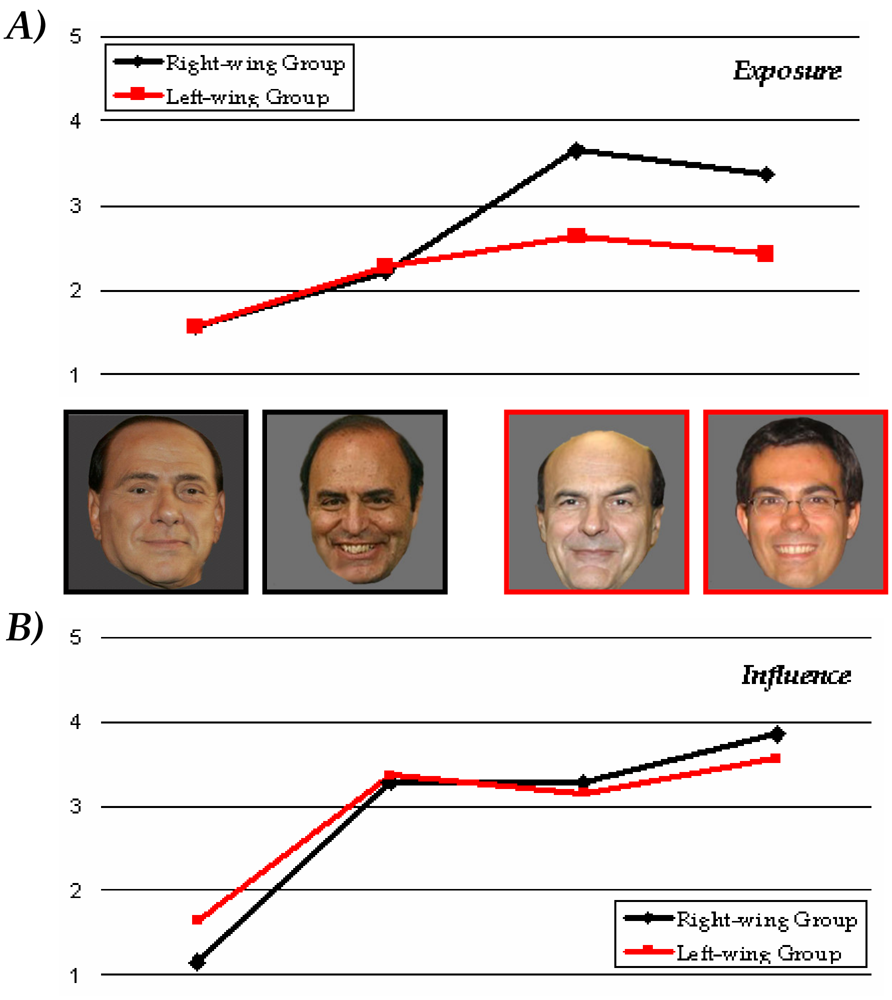


Figure 2: Ratings of Familiarity (Exposure) and Political Influence for In- and Out-group Characters. A) On the y axis, the Exposure scores, ranging from 1 ("I know him very well") to 5 ("I don't know him at all"). B) On the y axis, the Influence scores, ranging from 1 ("Very Influent") to 5 ("Not Influent at all"). On the x axis, right-wing character are depicted in a black square line (Berlusconi, Vespa) while left-wing characters are illustrated in red square line (Bersani, Floris). Scores for both Likert scales are reported for right- and left-wing participants.

The analysis of *Emotional Valence* scores revealed no significant main effect of each observed-face [F(3,26) = .568, n.s.] while a significant interaction between Observed-face and Group was found [F(3,26) = 34.299, p < .001]. Planned comparison revealed that right-wing participants rated as positive ingroup right- characters more than left-wing outgroup faces. Exactly the opposite emotional evaluation was expressed by left-wing participants who rated left-wing ingroup faces more positively than right-wing faces. This “positive ingroup bias” was confirmed by the fact that right-wing faces were evaluated as positive more by right- than left-wing group, and right-wing group judged left-wing characters as negative more than left-wing group did.

Perceived Similarity Questionnaire

To measure similarity, we asked participants to evaluate whether the following traits were applicable to each face: Energy/Extraversion, Agreeableness, Conscientiousness, Emotional stability, Intellect/Openness to experience. Than we computed an overall index representing the similarity between the self and each of the four personalities. A repeated-measures of variance with Observed-face (4 levels: Berlusconi/Vespa/Bersani/Floris) as within-participant factor and Group (right- or left-wing voters) as between-group factor revealed a main effect of Observed-face [F(3,27) = 3.812, p < .05]. Planned comparison showed that Berlusconi had higher perceived ratings than Vespa and Floris Opinion-makers. While Vespa only differed from right-wing leader as being evaluated as less similar than Berlusconi. No difference was found for Bersani with respect to the other face, while surprisingly Floris only differed from right-wing Leader being perceived more similar than Berlusconi. Importantly, a significant interaction between Observed-face and Group was found [F(3,26) = 31.170, p < .0001]. Planned comparison showed that right-wing voters perceived themselves as more similar to in-group faces (Berlusconi/Vespa) than did out-group faces (Bersani/Floris); exactly the opposite pattern was found for left-wing participants showing higher mean scores of similarity with Bersani and Floris than for Berlusconi and Vespa. These results are in line with the emotional valence scores seeing that participants judged as more similar to them, the characters with the same political orientation, showing a mere preferential “ingroup bias” for their political representatives.

Saccadic Performance in the scanning session.

Following previous studies [Kitagawa and Spence, 2005; Murphy and Klein, 1998; Spence et al., 2001a,b; Cazzato et al., 2010], we computed an inverse efficiency score by dividing, for each condition and in each subject, the mean correct RTs by the number of erroneous directionally responses. The inverse efficiency score provides a way to combine RT and accuracy measures of performance into a single measure [Townsend and Ashby, 1983] and allows controlling for any speed-accuracy trade-off effects. As for RT and error measures, higher inverse efficiency scores indicate worse performance. Table 1 reported Inverse efficiency scores as a function of the four O*bserved-face*: Berlusconi, Vespa, Bersani or Floris and *Congruence:* Congruent or Incongruent trials for Right- and Left-wing participants respectively.

The inverse efficiency score was entered in a 4 x 2 x 2 repeated-measure analysis of variance (ANOVA) with Observed-face (4 levels: Berlusconi / Vespa / Bersani / Floris) and Congruence (2 levels: congruent / incongruent) as 2 within-participant factors and Group (Right- / Left-wing voters) as between-group factor. A main effect of Condition [F (1,26) = 65.377, p < .001] was explained by the worse performance in the incongruent than congruent trials (444 vs. 525 ms/errors). No other effects or interactions were significant.

	Right-wing Voters		***Left-wing Voters***	
	Congruent	***Incongruent***	***Congruent***	***Incongruent***
Berlusconi	443.98	544.58	433.64	510.47
Vespa	450.52	543.51	440.07	501.21
Bersani	447.60	533.93	438.78	512.87
Floris	446.79	536.59	446.19	513.94

Table I. Behavioural performance during Gaze-following task. Inverse efficiency scores (mean RT/erroneous movement) are represented separately for Right- and Left-wing voters as a function of Observed-face [Berlusconi / Vespa / Bersani / Floris] and Condition [Congruent / Incongruent].

Since the analysis on behavioral performance was performed on a total of 5 fMRI runs (n = 720 trials), we cannot exclude that the "automaticity" of our critical gaze-following manipulation was affected by the duration of the total experiment and by the large number of trial. Therefore, additional analyses are required to verify whether reducing the number of observations may highlight the interaction we are looking for. Next step will be to compare the performance obtained from the experiment outside the scanner (Experiment 2) and that one obtained inside the scanner (Experiment 3) only considering the first fMRI run (n = 144 trial).

fMRI Results

For the first analysis, we tested for the overall conflict effect (Interference Effect, IE) between directional instructions provided by the colour central cues and the direction provided by the characters' gazes (irrespective of political affiliation of voters and observed-face) by subtracting incongruent minus congruent trials. On the other hand, to individuate brain responses correlating with the Face Observation effect (FO) (therefore those brain areas not specifically sensitive only to the conflict interest as tested in the previous analysis) relative to each observed-faces, we tested the main activation of congruent and incongruent trials in a main effect of observation. For both analysis, a regions of interest (ROIs) approach was applied by extracting average BOLD signals (MarsBar 0.41, 'MARSeille Boîte À Région d'Intérêt' SPM toolbox) from the peak activity of the voxels showing a main effect of Interference or a main effect of Observation. Each ROI was defined as a 10 mm radius sphere centred on the corresponding maxima of the whole-brain analysis, and p-values were Bonferroni-corrected. It should be noted that main effect and interaction contrasts are orthogonal and, therefore, our ROI selection procedure was unbiased (Friston et al., 1996).

Brain responses associated with the directional conflict between gaze and instruction signals: interference effect.

To identify areas associated with greater responses to the conflict between the directional instructions provided by the colour cues and the direction of the character saccade, we compared incongruent vs. congruent condition (Interference Effect: IE), collapsed over Group and Observed-face. For this comparison, the SPM threshold was set to p(FEW-corr) < 0.05 at voxel-level (cluster extent estimated a *p-uncorr* = 0.001, k = 62), considering the whole brain as the volume of interest (See table II).

Anatomical Area	**Cluster Size**	***p-corr***	**X**	**Y**	**Z**	**z scores**
Parietal Lobe						
R Precu	466	< .001	12	-58	58	4.84*
R SPL			18	-64	58	4.58*
R SMG	255	<.01	62	-38	38	4.06*
R STS			64	-40	24	3.85*
Frontal Lobe						
L FEF	418	<.001	-24	-2	58	4.74*
R SMA	958	<.001	18	0	62	4.63
R Mid Cingulum			8	20	36	3.98
L Insula	247	<.05	-32	20	6	3.84*
R Insula			34	22	8	4.06
L Lingual G	710	<.001	-10	-74	4	4.29

Table II. Mean MNI coordinates of activation foci associated with Incongruence Effect. Anatomical locations, peak coordinates in MNI space (Montreal Neurological Institute), and statistical values for the main effect of incongruence (incongruent > congruent trials, irrespective of Observed-face and Group). *p*-values are corrected for multiple comparisons at the cluster level, considering the whole brain as the volume of interest. R Precu= Right Precuneus; R SPL = Right Superior Parietal Lobule; R SMG = Right Supramarginal Gyrus; R STS = Right Superior Temporal Sulcus; R/L FEF= Right/Left Frontal Eye Field; R/L Insula= Right/Left Insula; R Cingulum Mid= Right Middle Cingulum; L Lingual G = left Lingual Gyrus. With the asterisk (*) we indicated the regions of interest (ROIs) within the dorsal fronto-parietal attentional network. ROIs were extracted averaging BOLD signals (see Methods) from a 10 mm sphere centred on the cluster peak.

As expected, this comparison produced mainly an extensive activation in the dorsal and central fronto-parietal attentional network including anterior frontal regions as the Middle Frontal Gyrus (MFG) namely the Frontal Eye Fields (FEF) bilaterally, and posterior parietal regions as the right Superior Parietal Lobule (SPL) and bilateral Precuneus (Corbetta and Shulman, 2002). Frontal regions also included the Superior Frontal Gyrus (SFG), the Supplementary Motor Area (SMA) extending to the middle portion of the Cingulate Cortex in the right hemisphere and left Insula. Furthermore, additional right parietal portion included Supramarginal Gyrus (SMG) extending to temporal region as Superior Temporal Sulcus (STS). Finally, a wide cluster in bilateral occipital areas spreading bilaterally from the Calcarine Scissure to the Lingual gyri was also activated (See Figure 2). No regions were obtained from the reverse contrast (“Facilitation effect”), even at a relaxed statistical threshold of $p < .005$.

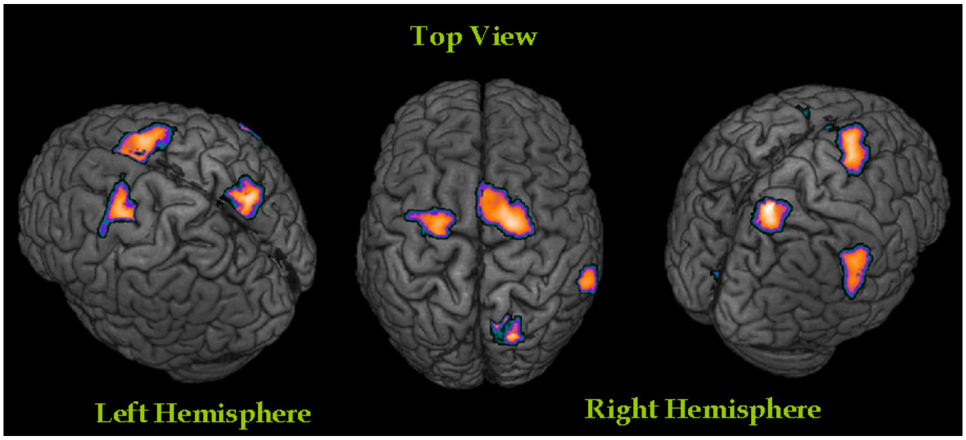


Figure 2: Brain regions activated by Interference Effect [Incongruent > Congruent trials]. Clusters showing higher activity in the incongruent than congruent condition irrespective of observed-faces and political affiliation of voters are rendered on 3-dimensional (3D) views of the SPM template. This contrast revealed the activation of dorsal and central attentional fronto-parietal networks. The regions included the Middle Frontal Gyrus (MFG) i.e. the Frontal Eye Fields (FEF) bilaterally, and posterior parietal regions as the right Superior Parietal Lobule (SPL) and bilateral Precuneus. Frontal regions also included the Superior Frontal Gyrus (SFG), the Supplementary Motor Area (SMA) extending to the middle portion of the Cingulate Cortex in the right hemisphere and left Insula. Furthermore, right parietal portion included Supramarginal Gyrus (SMG) extending to Superior Temporal Sulcus (STS). Finally, a wide cluster in bilateral occipital areas spreading bilaterally from the Calcarine Scissure to the Lingual gyri was also activated. These regions were used as regions of interest to assess any differential influence of distracter/instruction signal incongruence on the brain responses (SPM thresholds are set to p(FWE-*corr)* = 0.05 at voxel level).

First, to analyze the brain regions activated when participants performed a saccadic movements incongruently with respect to the gaze direction of Right-wing and Left-wing Characters, we tested for the interaction of IE x Right- or Left-wing Characters irrespective of leaders/Opinion-makers and Group [Effect of Political Affiliation of Characters]. No regions resulted specifically modulated by this interaction. Additional comparison showed that left FEF and right SPL reported a trend toward significance, being the IE greater for Ingroup faces in Left-wing voters [i.e. IE for Left-wing Faces in Left-wing group: left FEF: $t = 1.64$; $p = .052$; right SPL: $t = 1.58$; $p = .058$].

Next, we explored whether fronto-parietal regions are called into action when participants performed a saccadic movements incongruently with respect to the gaze direction of Leaders and Opinion-makers (irrespective to political party); thus we contrasted the fMRI signal between Leaders vs. Opinion-makers (i.e. IE[Leaders > Opinion-makers]). The interaction IE x Leaders surprisingly revealed no significant greater brain responses in the ROIs we investigated. To the opposite, when we tested for the interaction IE x Ingroup' Opinion-makers, several regions resulted specifically modulated (i.e. IE[Opinion-makers > Leaders]). For example, the IE in left FEF was greater for Opinion-makers than Leaders ($t = 1.85$, $p < .05$) and a trend toward significant was found specifically for Ingroup' Opinion-makers (irrespective of Left-wing Political Affiliation) (i.e. IE[Vespa > Floris] + [Floris > Vespa]; $t = 1.64$; $p = .053$). As well as left FEF, right SMG and right SPL showed a greater IE for Ingroup' Opinion Makers (right SMG: $t = 2.45$; $p = .008$; right SPL: $t = 2.19$; $p = .015$).

Additional comparison, confirmed that this effect in right SMG was due to a greater IE for Ingroup' Opinion-maker in Left-wing Voters (i.e. IE[Floris > Vespa]; t = 2.84, p = .003]. Finally, Left Insula resulted specifically modulated only for Right-wing voters by the interaction IE x Opinion-maker x Group (i.e. IE[Vespa + Floris] > [Berlusconi > Bersani]; t = 1.88, p = .038). Additional comparison revealed that this effect in left Insula was only specific for: ingroup Opinion-makers (i.e. IE[Vespa > Floris] + [Floris > Vespa]; t = 2.02; p = .023) and most important for Right-wing Opinion-maker (Bruno Vespa) in Right-wing voters (i.e. IE[Vespa > Floris] in Right-wing Group; t = 1.83, p = .035). Finally, we hypothesized that our manipulations of IE would affect neural responses within the dorsal fronto-parietal attentional systems, depending on specific relationships with *Observed-face* and *Political Affiliation* of voters (Group). To test this prediction, we analysed the differences in brain responses when participants performed saccadic movements incongruently with respect to the gaze direction of Leader and Opinion-makers belonging to the "Same" political party. In other words, we were interested in testing the specific interference effect of gazes belonging to the same political party, namely the IE for "Ingroup characters". The unique region of interest resulting specifically modulated by the interaction IE x Observed-face x "Same" Political Affiliation of voters was left FEF (i.e. IE([Berlusconi + Vespa] > [Bersani + Floris] + [Bersani + Floris] > [Berlusconi + Vespa]); t = 2.05, p = .021). The result is illustrated in Figure 3. No other ROI approached the significance for the IE of "Ingroup Bias" contrast.

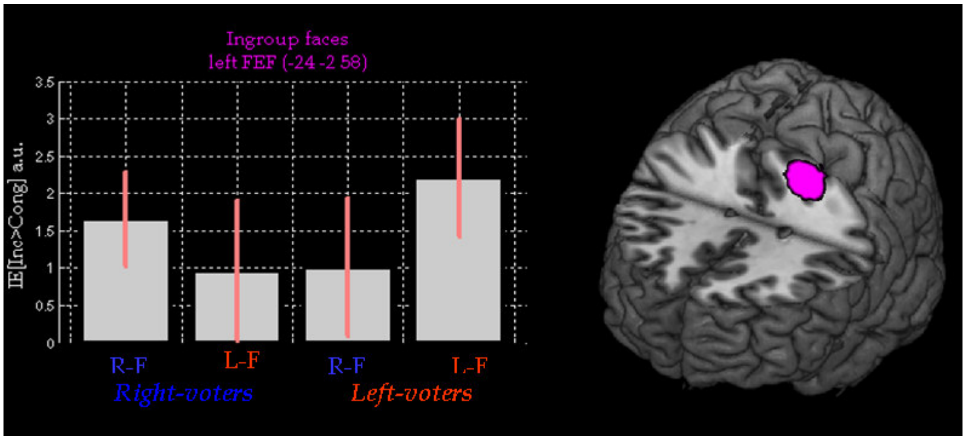


Figure 3: Brain responses in left Frontal Eye Field elicited d by the Interference Effect of Ingroup Left- and Right-wing characters. Right panel: 3D rendering of the canonical MNI template showing the localization of the region of interest (ROI) corresponding to the left (pink) frontal eye field [FEF] is reported in the coronal section. Left panel: the relative plot shows the mean Interference Effect [IE(inc<cong)] of the Right- and Left-wing Faces in Right- and Left-wing participants. A significant interaction was observed in this ROI: Right-wing Ingroup faces [R-F = Right-wing Faces] interfered on shifts of attention more than the Outgroup Left-wing faces [L-F = Left-wing faces] distracter. Exactly the opposite pattern was found for Left-wing voters. The level of activation is expressed in arbitrary units (a.u., ±90% confidence interval).

Correlations with "Perceived Similarity Scores"

To further understand the relationship between subjects' perceived similarity responses relative to ingroup characters and their brain activity, we looked at how their subjective ratings of the Leaders and Opinion-makers correlated with their brain activity while performing incongruent saccadic movements with respect to ingroup gazes. Surprisingly, only in Left-wing voters, activation in right SMG and left IPL (MNI coordinates of peak voxel: -56, -24, 50, data not shown) was greater during gaze-following shifts towards left-wing ingroup characters' gaze with whom participants more strongly associated themselves (with respect the outgroup political members). That is, left-wing participants perceiving themselves as "similar to ingroup" demonstrated greater engagement of right SMG and left IPL as a function of IE for ingroup character (more than right-wing outgroup characters). In Figure 4, we only depicted the positive correlation between Ingroup "Perceived Similarity scores" (compared to outgroup characters) and the relative IE for ingroup characters in right SMG (t = 3.31; p < .001).

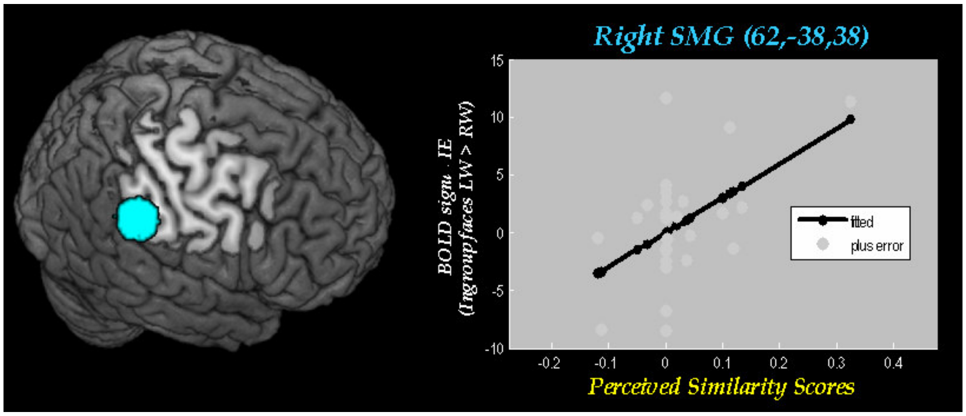


Figure 4: Scatter plot displaying the relation between BOLD responses and "Perceived Similarity Scores" in Right Supramarginal Gyrus for Left-wing Participants. The x axis displays the "Perceived Similarity score" difference calculated by subtracting the scores for ingroup left-wing faces minus the scores for outgroup right-wing faces for left-wing voters (higher values indicate stronger perceived similarity with respect to own ingroup characters). The y axis displays the difference of the parameter estimate associated with incongruent trials minus the

parameter estimate associated with congruent trials for ingroup left- larger than right-wing outgroup faces in left-wing voters (thus, greater values indicate grater IE for left- faces more than for right-wing faces). In right SMG, left-wing voters who perceived themselves more similar to ingroup than outgroup also showed larger BOLD response (Interference Effect) while performing saccadic movements incongruently with respect to the gaze direction of their political representatives (with respect to the outgroup characters).

Brain responses associated with the "observation" of Gaze irrespective of directional conflict between directional gaze and instruction signals: Face Observation effect.

To identify areas associated with greater brain responses, irrespective of the "conflict" between the directional instructions provided by the colour cues and the direction of the character's saccade, we performed a two-sample t-test analysis. By testing the main effect of Observation, we aimed at identifying the brain regions activated by the mean of incongruent and congruent condition (Face Observation: FO), collapsed over Group and Observed-faces. For this comparison, the SPM threshold was set to p(FEW-corr) < 0.05 at voxel-level (cluster extent estimated a *p-uncorr* = 0.001, k = 180), considering the whole brain as the volume of interest (See Table III). As for the IE analysis, first we extracted average BOLD signal from the peak activity of the voxels showing a main effect of FO, second we tested our interaction on a flexible factorial model (again by using MarsBar). Because, this analysis was not based on a differential effect as for IE analysis (i.e. incongruent > congruent trials) but instead took into account the mean activation of congruent and incongruent trials, we observed strong and extensive activation not only in the dorsal fronto-parietal network but also in the occipital visual cortex (See Figure 5).

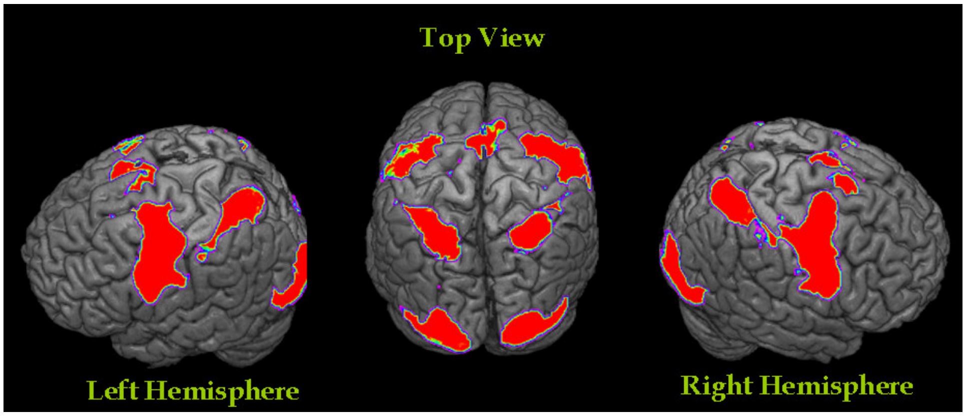


Figure 5: Brain regions activated by Observation Effect [Incongruent + Congruent trials]. Clusters showing higher activity in the incongruent plus congruent condition irrespective of observed-faces and political affiliation of voters are rendered on 3-dimensional (3D) views of the SPM template. This comparison revealed a wide cluster in bilateral Inferior Occipital Gyri extending to right middle temporal gyrus occipital region. In the frontal lobe, we found an extensive cluster in Precentral and Middle frontal gyri (including FEF) extending bilaterally in right and left hemispheres. Parietal regions included significant activation in superior and inferior parietal lobe only in Left Hemisphere. Finally, a significant cluster was found in Left Insula including left Putamen. These regions were used as regions of interest to assess any interaction between the observation of character according to the same or different political affiliation. (SPM thresholds are set to p(FWE-*corr)* = 0.05 at voxel level).

As shown in Table 3, this comparison revealed a wide cluster in bilateral Inferior Occipital Gyri extending to right middle temporal gyrus occipital region. In the frontal lobe, we found an extensive cluster in Precentral and Middle frontal gyri (including FEF) extending bilaterally into right and left hemispheres. Parietal regions included significant activation in superior and inferior parietal lobe only in Left Hemisphere. Finally, a significant cluster was found in the Left Insula including left Putamen.

Anatomical Area	**Cluster Size**	***p-corr***	**x**	**Y**	**Z**	**Z Scores**
Occipital Lobe						
R Occipital Inf	1673	< .000	24	-96	2	7.18
R Temporal Mid			42	-68	0	4.15
L Occipital Inf	1952	<.000	-20	-98	-6	7.07
Frontal Lobe						
L Precentral G	10868	<.000	-56	6	34	6.92*
R Precentral G			54	0	48	6.66*
Parietal Lobe						
L SPL	2442	<.000	-34	-54	60	5.77*
L IPS			-34	-46	50	5.74*
L Insula	322	<.001	-30	20	6	4.80*
L Putamen			-24	4	10	3.60

Table III. Mean MNI coordinates of activation foci associated with Observation Effect. Anatomical locations, peak coordinates in MNI space (Montreal Neurological Institute), and statistical values for the main effect of Observation (incongruent + congruent trials, irrespective of Observed-face and Group). *p*-values are corrected for multiple comparisons at cluster level, considering the whole brain as the volume of interest. R/L Occipital Inf = Right/Left Occipital Inferior Gyrus; R Temporal Mid = right middle temporal gyrus; R/L Precentral G = Right/left Frontal Precentral Gyrus; L SPL = Left Superior Parietal Lobule; L IPS = Left Intraparietal Sulcus; L Insula = Left Insula; L Putamen = Left Putamen. With the asterisk (*) we indicated the regions of interest (ROIs) within the dorsal fronto-parietal attentional network. ROIs were extracted averaging BOLD signals (see Methods) from a 10 mm sphere centred on the cluster peak.

Using the same procedure as outlined in IE analysis, we explored the brain regions activated when participants “observed” the gaze direction of Right-wing Characters with respect to Left-wing Characters [Political Affiliation of Observed-faces]. Thus, we tested for the interaction of FO x Right- or Left-wing Characters irrespective of Leaders/Opinion-makers and Group. No regions resulted specifically modulated by this interaction. Indeed, neither specific modulation of FO Left- or Right-wing face, nor greater FO for Left- more than Right-wing faces (and vice versa) with respect to political affiliation of voters were found.

Next, we explored whether the observation of Leaders with respect to Opinion-makers could elicit larger BOLD responses in our participants. Therefore, irrespective of political party, we contrasted the BOLD signal between Leaders and Opinion-makers (i.e. FO[Leaders > Opinion-makers]). The interaction FO x Leaders surprisingly revealed a significant greater brain responses in left SPL and IPS, and bilateral Precentral Gyri ROIs (i.e. (FO([Berlusconi + Bersani]) > [Vespa + Floris]) + (FO([Bersani + Berlusconi] > [Floris + Vespa]); L SPL: t = 3.07, p = .001; L IPS: t = 3.15, p = 001; R Precentral Gyrus: t = 1.69, p = .047; L Precentral Gyrus: t = 1.97, p = .03). Additional comparison showed that this effect was due to a significant interaction of FO x Leaders x Group specifically for the Right-wing voters (i.e. (FO[Berlusconi + Bersani]) > (FO[Vespa + Floris]) in Right-wing Voters); L SPL: t = 2.13, p = .019; L IPS: t = 2.35, p = .011). A trend toward significance was shown only in Left Precentral Gyrus for the same interaction (t = 1.58, p = .059). The same interaction of FO x Leaders x Group specifically for the Left-wing voters (i.e. (FO[Bersani + Berlusconi]) > (FO[Floris + Vespa]) in Left-wing Voters) was confirmed only in the left parietal ROIs: L SPL: t = 2.22, p = .015; L IPS: t = 2.17, p = .017).

To further explore the BOLD responses specifically associated with the Ingroup' Leader FO effect, we investigated the interaction FO x Leader, with respect of Ingroup Leaders (i.e. (FO([Berlusconi > Bersani]) + (FO([Bersani > Berlusconi])). Only Left SPL ROI resulted specifically modulated by this interaction (t = 1.66, p = .05). An additional contrast confirmed that this effect in Left SPL was due to a significant FO effect only for Ingroup Leader in right-wing participants (i.e. FO[Berlusconi > Bersani] in Right-wing participants); t = 2.45, p = 008). Finally, a crucial contrast testing for the Leadership of Berlusconi in right-wing voters (i.e. (FO[Berlusconi > Vespa]) > (FO[Bersani

> Floris])) striking confirmed that this effect was reflected in both left Parietal regions (L SPL: t = 2.77, p = .003; L IPS: t = 2.35, p = .011) (See Figure 6).

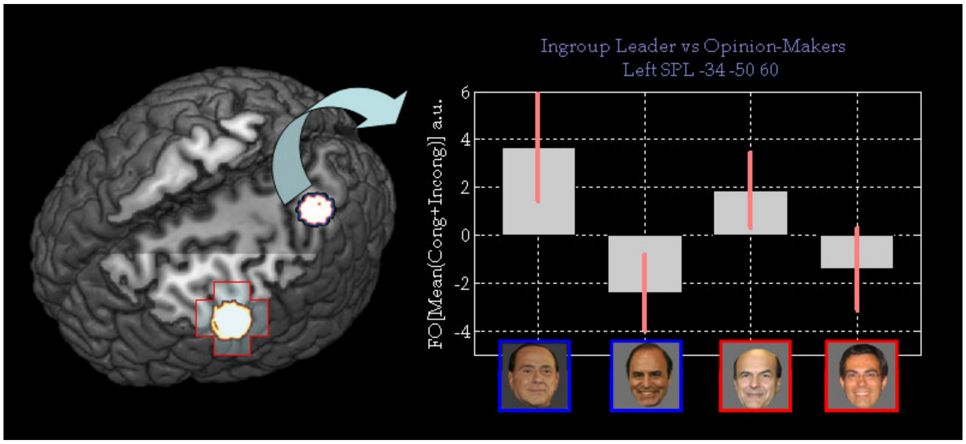


Figure 6: Brain responses in left Superior Parietal Lobe elicited by the "Observation" of Ingroup and Outgroup Faces only in Right-wing voters. Left panel: 3D rendering of the canonical MNI template showing the localization of regions of interest (ROIs) corresponding to the Left (yellow) Precentral gyrus centred on [-56 -6 34] peak and left (blue) is reported in the axial section. Right panel: the plot shows the mean Face Observation effect [FO(inc + cong)] of the Right- and Left-wing Faces in Right-wing participants only for Left SPL. We depicted a "cross" on Left Precentral Gyrus to indicate no significant modulation for this area. A significant interaction was observed in L SPL ROI: Right-wing Ingroup faces enhanced greater FO effect more than outgroup left-wing faces. Interestingly, this effect was also specific and greater for Right-wing Leader Berlusconi than ingroup Opinion-maker and Outgroup Faces. The level of activation is expressed in arbitrary units (a.u., ±90% confidence interval).

On the contrary, when we tested for the interaction FO x Opinion-makers with respect to the Leaders and taking into account the political affiliation of voters, no regions of interest resulted significantly modulated (i.e. (FO[Opinion-makers] > [Leaders]).

Finally, we aimed to test whether the "observation" of gaze belonging to the same political party, namely the FO for "Ingroup characters" could elicit greater BOLD responses in the ROIs mentioned above. None of the ROIs approached the significance for the FO of "Ingroup Characters", highlighting the core role of left FEF in controlling and inhibiting the proneness of gaze-following behavior with respect to your own ingroup member, as shown by the Interference Effect analysis.

Discussion

The aims of this study were to 1) explore how the gaze of a Political Leader or an Opinion-maker may interfere with saccadic movements of an onlooker; 2) clarify whether high-order social variables such as the political affiliation could modulate reflexive joint attention mechanism; 3) answer to the following questions: "How does the "personological similarity" between a ingroup character and a voter interfere with reflexive shifting of attentional mechanism?"; and finally, "Does this personality dimension correlate with the magnitude of this interferential effect?".

Although participants were instructed to ignore distracting gaze of each political character and to focus only on the instructions provided by the central cue, a cost to reorient in incongruent trials irrespective of Observed-face and Group was found. At behavioral level, the absence of the significant 3-way interaction of Group x Observed-face x Congruence may be explained by the fact that, compared to the behavioral study outside the scanner, the fMRI experiment contains long sessions of trials. Therefore two main potential explanations may minimize the automatic effect: first, the adaptation effect along the five functional runs may have obscured the automatic effect even if our paradigm comprises a datasets of three different pictures for each observed face. Second, the long duration we need to acquire meaningful fMRI data, may induce expectation effect in participants again minimizing the reflexive effect of joint attention. As mentioned before, next step will be to isolate the performance obtained from the first functional run in order to verify the robustness of gaze following behavior by comparing the experiments inside and outside the scanner. Although somewhat preliminary, we found that brain responses of interference effect according to political affiliation of voters and ingroup characters were reflected in the activation of the dorsal Fronto-parietal network. In particular, we observed a modulation of left FEF for ingroup characters according to the same political party. Such interference effect was also found to be significant for ingroup media opinion-makers. In the R SMG again a specific modulation was found for ingroup media opinion-makers and specifically for the ingroup left-wing Opinion-maker (Giovanni Floris). Interestingly, these results were found to positively correlate with ingroup perceived similarity only for left-wing voters. Although no behavioral main effect seems to suggest difference in our sample group, further analysis are required to verify if these differences specifically found for the left-wing voters may rely on other personality or emotional dimensions. Ongoing analysis on pure face observation effect seems to suggest a difference between left and right-wing voters in the processing of the “ethological social meaning” of the gaze provided by their relative ingroup characters. We can speculated that left

FEF is more engaged in left-wing voters while performing saccadic movements with respect of incongruent gaze of ingroup characters, thus left-wing voters may be more prone to “mentalize” (See Chapter 2 for an exhaustive explanation of joint attention and ToM) with their own ingroup members than with the outgroup. One may speculate that left-wing voters are more prone to infer the mental states or the intention to communicate something important by looking and following the gaze of their political ingroup. On the contrary, right-wing voters seem to process only the “saliency” in terms of social identity of their ingroup representatives, without being sensitive to the interference effect. This relation is expressed by the BOLD responses observed in Parietal ROIs (left SPL and IPS) by means of the FO contrasts. However, further (still in process) analyses are required to verify these issues for example by analysing separately the two groups and correlating their brain responses to self-reports and personality scales.

Future Directions

Reflexive social attention mediated by gaze-observation: role of the perceived fairness of others induced by economic interactions

By means of the gaze-cuing paradigm, we intend to investigate the attentional shifting mediated by other's gaze when two individuals are playing an economic game. The main novelty of the present study consists in exploring whether reflexive shifts of joint attention in an onlooker are specifically influenced by the gaze of models who are perceived (by the onlooker) as fair or unfair on the basis of their previous interaction in an economic game**.** In this direction, Neuroeconomics reported that economic decisions are influenced by the way an individual perceives a "proposer model" that make a monetary offer. This happens in relation to personality traits such as altruism or selfishness, allowing to establish an emphatic relationship, rather than a revenge, and depends on the perceived personality of the model.

Classical "Theory of economic decision-making" assumes that people should behave rationally, maximizing gains and minimizing losses. On the contrary, previous studies reported that in the *Ultimatum Game*, as well as in other economic contexts, this assumption is systematically violated. In this game, two players have to split a sum of money. One player acts as *Proposer*, who suggests how the money should be divided between the *Proposer* and the *Decisor*. The second player – playing as the Decisor – has to decide whether to accept or to reject the offer. If the Decisor accepts the offer, both players gain the amount agreed upon. If the Decisor rejects the offer, neither participant receives anything. A perfectly rational Proposer should make the smallest possible offer to maximize his/her gain, while a perfectly rational Decisor should accept any offer since – in economic terms – even a small amount is better than gaining nothing. In reality, however, players systematically do not conform to these predictions: Proposer makes equal/fair offers (such as 50:50 or 60:40) because they are more likely to be accepted, and responders reject unequal/unfair offers (such as 90:10 or 80:20) to "punish" the Proposer and to motivate him/her to make fairer offers. This kind of behavior realizes a sort of "altruistic punishment", a lesson of "good behavior" for the social group benefit in comparison of an individual reputed egoist, even if this action leads to a personal disadvantage. Numerous behavioral and self-report studies using the ultimatum game have established that people dislike unfair treatment.

For example, as stinginess of an offer relative to the stake size increases, a self-reported feeling of contempt also increases, as does the likelihood to reject the offer. Similarly, unfair offers that are rejected tend to elicit activity in the anterior insula, and the more likely a person is to reject unfair offers, the more activity this insula region exhibits.

Sanfey and collaborators used functional magnetic resonance imaging (fMRI) to monitor the brain activity of responders while playing ultimatum games. Those who showed greater activation in the bilateral anterior insula, a part of the brain associated with negative emotions, were more likely to reject unfair offers. Those who showed greater activation in the dorsolateral prefrontal cortex, an area linked to problem solving and cognitive conflict, were more likely to accept unfair offers. In an fMRI study, McCabe et al. studied brain activation in humans who played sequential two-person simplified Ultimatum Games for cash rewards. Half of the time, subjects played as player 1, the other half as player 2. Each time they played, their counterpart was either a computer playing a fixed probabilistic strategy or a human who was recruited to play outside the scanner. Subjects were told for each play whether they were playing the computer or the human. The authors conjectured that subjects would use "mentalizing" to infer the intentions of the other player. Mentalizing would play an important role in the binding of mutual pay-off information to a cooperative event representation and thus invoke cognitive strategies to delay gratification, and therefore induce trust and reciprocity. Recent research has shown that the arMFC is not only involved in representing our own thoughts, feelings and beliefs, but also in representing the mental states of other people, and is activated in a variety of social cognition tasks such as self-knowledge, person perception and mentalizing (for a review see Amodio & Frith, 2006). The authors argue that the observed activation in cooperators is consistent with shared reciprocity intentions, resulting in the inhibition of both individual reward seeking by player 2 and risk avoiding behaviour by player 1.

The present project aims to explore mechanisms and neural underpinnings of reflexive joint attention triggered in an onlooker by the interfering gaze of individuals who are perceived as fair or unfair. Fair/unfair perception will be induced by asking to confederate subjects *(Proposer)* to play fairly or unfairly in an economic decision game largely used in neuroscience studies, namely the

Ultimatum Game. “The Ultimatum Game illustrates the tension between economic self-interest, on the one hand, and reciprocity and equity motives, on the other”. In this game, two anonymous individuals, a proposer and a responder (experimental subject), have to agree on the division of a given amount of money, say $20, according to the following rules: The proposer can make exactly one suggestion on how the $20 should be allocated between the two by making an integer offer X to the responder. Then the responders can either accept or reject X. In case of a rejection, both players earn $0; in case of acceptance, the responder earns X and the proposer earns $20 – X. If economic self-interest alone motivates the responder, he will accept even a very low offer, say $1, because $1 is better than $0. However, if concerns for reciprocity and equity motivate him, he might reject low offers because he views them as insultingly unfair and inequitable. The responder thus faces a conflict in case of low offers between his economic self-interest, which encourages him to accept the offer, and his fairness goals, which drive him toward rejecting it. Strong evidence suggests that many people reject low offers in the game, even if stake levels are as high as 3 months’ income. Rejection rates up to 80% have been observed for offers below 25% of the available money.

We aim to address the hypothesis that social factors and personality traits as fairness or trustworthiness, strongly influence the economic decision-making process and the shifting of reflexive joint attention induced by the individual who provides the interfering gaze, in this case the Proposer, and the individual who is influenced by the gaze, the Decisor. Drawing on this series of experiments, we plan to test the hypothesis that, the social status attributed to the Decisor-player influences his capability to shift the attention of the onlooker-Decisor. We further expect that, also reflexive attentional orienting considered as an automatic process, when it is induced by a player's gaze perceived as a fair/unfair model, may reflect the relation hypothesized above (i.e. the interfering effect is bigger when Proposer-Player is perceived as a fair/unfair model than a neutral condition by the Decisor). Therefore, our objective is to investigate whether an automatic behavior such as reflexive joint attention may be modulated at an (unconscious) unaware level as a function of the perceived unfairness of a player-Proposer. In our paradigm, participants (always Decisor) have to accept or reject the monetary offers of a Proposer that tries to negotiate an equal/unequal offer. In a second phase, inside the fMRI scanner, participants/Decisor will attend the saccadic task by means of joint attention paradigm, in which the interfering and distracting gaze would be that one perceived as fair/unfair or neutral Proposer-player.

In line with the current literature, we aim at replicate the well-documented pattern of accepting fair offers and increasing the rate of rejection as offers become less fair. Therefore, we predict a bigger rejection rate during the economic exchange between the Decisor and the unfair/egoist Proposer. In contrast, a model perceived as fair/benevolent should be rated as more trustworthy than the unfair model, thus receiving more acceptance offers even in case of low offers. We do not expect any difference in the case of the neutral condition (i.e. Lottery) in which the gaze presented as Proposer has no moral responsibility about the offers (in this case a PC will make random offers thus presenting both fair and unfair offers). In the crucial gaze-cuing task, we hypothesized an oculomotor interfering effect produced by the fair/unfair Proposer-model with respect to the neutral Proposer-model. In particular, we expect to find a larger gaze interfering effect when the Decisor perceives the Proposer as an unfair model than on the neutral condition. Therefore, the interfering effect of gaze on saccadic movement would be higher when the participant feel himself frustrated because of Proposer's unfair behavior. We have no specific prediction about the direction of the interference: the Decisor onlooker may follow or avoid the direction shown by the fair/unfair gaze based on the inference that the indicated direction may signal a potential danger or a source of reward. Capitalizing on such behavioural expectations we will try to determine whether the neural activity in the network underpinning the observation of an interfering gaze may be modulate by the type of perceived fair/unfair model. We will record changes of BOLD fMRI signal associated to conditions where the three different perceived models influence overt directional saccades triggered by central instruction signals. We predict a specific involvement of dorsal frontoparietal structures in modulating attentional shifts triggered by directional, socially relevant stimuli (i.e. eyes). Moreover, we predict more interference of gaze belonging to fair/unfair models than the neutral one. This would suggest that the tendency of an onlooker (Decisor) to imitate the actions of the observed fair/unfair model (Proposer) reflects the activity of a resonant system that works according to how we perceive the person we interact as trustworthy or selfish. Moreover, in accordance with "theories of inequity aversion" (Fehr & Schmidt, 1999), we expected to observe enhanced activity in brain areas not only involved in attentional and execution mechanism relative to saccadic movement per se, but also areas related to emotions and reward processing (bilateral anterior insula, ACC, ventral striatum and OFC) in response to unfair offers of human partners in the Ultimatum Game. In contrast, we predict an enhanced activity in reward-related areas such as striatum, rostral ACC, and OFC during mutual cooperation between the participants and the "fair model-Proposer". Moreover, we expect activity in Striatum and rostral ACC solely when Decisor playing with human but not computer partners. On theoretical and empirical grounds, we predict that the face of a fair or unfair person would elicit "automatic" emotional non responses reflecting evaluative processes. Furthermore, we expect to find brain circuitry related to social cognition including the Amygdala, orbitofrontal cortex, striatum, insula, Fusiform gyrus, and superior temporal sulcus, implicated in the perception of defectors as well as cooperators. The results will allow to explore whether the neural underpinnings of an automatic behaviour like "reflexive joint attention" can be implicitly modulated by the perceived personality of the gazing player individual.

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