Seeing It My Way or Your Way: Frontoparietal Brain Areas Sustain Viewpoint-independent Perspective Selection Processes

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Abstract

■ A hallmark of human social interaction is the ability to consider other people's mental states, such as what they see, believe, or desire. Prior neuroimaging research has predominantly investigated the neural mechanisms involved in computing one's own or another person's perspective and largely ignored the question of perspective selection. That is, which brain regions are engaged in the process of selecting between self and other perspectives? To address this question, the current fMRI study used a behavioral paradigm that required participants to select between competing visual perspectives. We provide two main extensions to current knowledge. First, we demonstrate that brain regions within dorsolateral prefrontal and parietal cortices respond in a viewpoint-independent manner during the selection of task-relevant over task-irrelevant perspectives. More specifically, following the computation of

two competing visual perspectives, common regions of frontoparietal cortex are engaged to select one's own viewpoint over another's as well as select another's viewpoint over one's own. Second, in the absence of conflict between the content of competing perspectives, we showed a reduced engagement of frontoparietal cortex when judging another's visual perspective relative to one's own. This latter finding provides the first brain-based evidence for the hypothesis that, in some situations, another person's perspective is automatically and effortlessly computed, and thus, less cognitive control is required to select it over one's own perspective. In doing so, we provide stronger evidence for the claim that we not only automatically compute what other people see but also, in some cases, we compute this even before we are explicitly aware of our own perspective. ■

INTRODUCTION

One remarkable feature of our social abilities is that we are not only able to reflect on our own mental states, such as our desires and intentions, but we can also have some insight into other people's mental lives. The awareness of one's own and other people's perspectives as well as the ability to shift between them are fundamental processes that guide how we interact with other people. One question that has interested researchers for several years now is how perspective taking is achieved in the human brain. Prior neuroimaging studies have focused on brain systems involved in attributing perspectives to oneself or another person and largely ignored the neural mechanisms that select between self and other perspectives. Here we examine which brain regions are involved in selecting between self and other visual perspectives using fMRI.

The ability to consider the content of another person's mental state, such as what they see, believe, or desire is commonly referred to as a "theory-of-mind" (ToM) judgment (Premack & Woodruff, 1978). It has been suggested that ToM judgments involve two distinct cognitive

mechanisms: computation and selection (Leslie, German, & Polizzi, 2005; Leslie & Thaiss, 1992). The first mechanism generates candidate mental state contents, such as what someone believes or what they can see, whereas the second reviews these candidates and signals which perspective to select (Leslie et al., 2005). Because our own beliefs and visual perceptions often diverge from the perspective of others, we must consider the relationship between our own and other people's mental state contents to guide everyday social interactions. Importantly, the situational context determines which perspective or whose perspective is relevant, and it is perspective selection processes that bias or prioritize the relevant perspective to use.

To date, the majority of behavioral research investigating perspective taking has focused on the computation and selection of another's perspective while inhibiting one's own viewpoint. This research has suggested that taking someone else's perspective is cognitively costly (as measured by increased RTs and errors; Kessler & Thomson, 2010) and requires resisting interference from one's own perspective (Samson, Apperly, Kathirgamanathan, & Humphreys, 2005). For example, when asked explicitly about other people's perspective, young children tend to give egocentric responses (Wellman, Cross, & Watson,

2001) but become less egocentric as they develop their cognitive control abilities (Carlson, Moses, & Breton, 2002; Carlson & Moses, 2001; Ozonoff, Pennington, & Rogers, 1991). Adults also show egocentric biases when taking someone else's perspective (Birch & Bloom, 2004, 2007; Keysar, Lin, & Barr, 2003; Keysar, Barr, Balin, & Brauner, 2000), and these biases are exacerbated when they are under cognitive load (Epley, Keysar, Van Boven, & Gilovich, 2004). Thus, the egocentric viewpoint has been suggested to be the default perspective for encoding external information (Shelton & McNamara, 1997, 2001) and the basis for reasoning about others' mental states (Epley et al., 2004).

More recent findings, however, suggest that taking another person's perspective can be easy and effortless under some circumstances. For example, despite limited cognitive resources, infants and chimpanzees expect that others will behave in accordance with what they have seen, even when that visual perspective conflicts with their own viewpoint (for reviews, see Baillargeon, Scott, & He, 2010; Call & Tomasello, 2008; Emery & Clayton, 2004). For example, 15-month-old infants expect an observed agent to behave in accordance with where the agent falsely believes a toy to be hidden, even when the infants know the toy's actual location (Onishi & Baillargeon, 2005). This evidence has been taken to suggest that infants have an innate or early-developing sensitivity to other people's knowledge and belief states, which operates without explicit instruction and with minimal cognitive resources (Baillargeon et al., 2010; Gergely & Csibra, 2003; Leslie, 1994).

Furthermore, adults sometimes compute another's visual perspective and belief state in an effortless and automatic manner. That is, another person's viewpoint is computed without instruction to do so (Back & Apperly, 2010; Cohen & German, 2009, 2010) and even when its computation is task-irrelevant and interferes with performance (Surtees & Apperly, 2012; Surtees, Butterfill, & Apperly, 2011; Kovács, Téglás, & Endress, 2010; Qureshi, Apperly, & Samson, 2010; Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010). For example, using a visual perspective taking task, Samson and colleagues showed the co-occurrence of two types of interference in participants' judgments: egocentric and altercentric. When explicitly judging what another person could see, participants were influenced by what they themselves could see, which is indicative of egocentric interference (Birch & Bloom, 2004; Keysar et al., 2003). More surprisingly, when simply instructed to judge what they themselves could see, participants were influenced by what the other person could see, which is indicative of altercentric interference. The emergence of evidence for altercentric interference demonstrates that without any instruction to do so and at a cost to one's own performance, adults still compute other people's perspectives (i.e., they remain sensitive to what the other person can see). These data point toward the view that the processes involved in reasoning about others' visual perspectives and beliefs

may have at least one automatic quality: unintentionality (Bargh, 1994).

Subsequent work using the task developed by Samson and colleagues (2010) has demonstrated that both types of interference (egocentric and altercentric) are exacerbated under conditions of cognitive load, whereas neither perspective computation is influenced by the same cognitive load (Qureshi et al., 2010). These results suggest that participants automatically and effortlessly compute both what they and the other person can see (even under cognitive load), but that the selection of the relevant perspective is effortful (as the two interference effects increased under cognitive load). Furthermore, the findings are consistent with the view that selecting the relevant perspective is cognitively demanding (cf. Leslie et al., 2005) and may involve a common process for taking one's own perspective (and inhibiting another person's perspective) as well as taking another person's perspective (and inhibiting one's own perspective).

Insight into the neural bases underlying perspective taking abilities has been recently provided through human neuroimaging experiments. The results of these experiments have demonstrated that representations of self and other involve both common and distinct brain regions (for a review, see Zaki & Ochsner, 2011). Common patterns of activation consistently reflect similarities in the content of what is represented for self and other; that is, activation of sensory, motor, spatial or emotional information, depending on the nature of the task (Keysers & Gazzola, 2009; Decety & Grézes, 2006; Decety & Sommerville, 2003). Such overlap in activation patterns for self and other span a wide range of phenomena, including pain, disgust, action, touch, and mental state reasoning (Keysers & Gazzola, 2009; Decety & Grézes, 2006). Together, these results suggest that common neurocognitive mechanisms may be engaged when processing information relating to one's own experiences as well as the experiences of others.

The neural regions engaged when making judgments of self and other are not identical, however, and distinct patterns are also observed suggesting that some aspects of self and other representations involve unique processes (Zaki & Ochsner, 2011; Northoff et al., 2006; Northoff & Bermpohl, 2004; Decety & Sommerville, 2003; Vogeley & Fink, 2003). For example, in simple visual perspective taking tasks, brain regions associated with self more than other include anterior medial frontal, posterior cingulate, and insula cortices, whereas the inverse contrast has been associated with activity in both dorsomedial and dorsolateral frontoparietal cortex as well as temporo-parietal cortices (Schnell, Bluschke, Konradt, & Walter, 2011; Corradi-Dell'Acqua et al., 2008; David et al., 2006, 2008; Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006; Vogeley et al., 2004). It has been suggested that when judging another's visual perspective lateral prefrontal cortex (lPFC) inhibits one's own irrelevant perspective (Shibata & Inui, 2011), whereas temporo-parietal cortices discriminate self

from other in cases of perspective conflict (Shibata & Inui, 2011; Corradi-Dell'Acqua et al., 2008; Aichhorn et al., 2006; Jeannerod, 2004; Decety & Sommerville, 2003).

Although these prior neuroimaging studies illustrate the brain regions involved in self and other representations, it is not yet clear which brain regions are recruited to select the relevant over the irrelevant perspective. More specifically, a limitation of prior fMRI research is that perspective computation and selection processes are often confounded in contrasts between self and other. For example, brain regions identified through direct comparisons between self-oriented and other-oriented judgments could reflect the computation of the relevant perspective and/or the prioritizing of the relevant over the irrelevant perspective. Moreover, it is not known whether brain regions involved in selecting the self-perspective over the other-perspective are the same as the ones involved in selecting the other-perspective over the self-perspective. Thus, it is not known if the process of perspective selection has a common neural basis for self and other.

A further issue that has so far received little attention relates to the neural processes engaged when another's viewpoint is automatically adopted. Considering the proposed primacy of the egocentric viewpoint (Epley et al., 2004; Shelton & McNamara, 1997, 2001), it is surprising that under certain circumstances (when the content of visual perspectives are consistent between self and other), participants are significantly quicker at judging the other person's perspective than their own perspective (Samson et al., 2010). This finding suggests that, at least in some circumstances, adopting another's perspective is less cognitively demanding and thus less dependent on top–down control than selection of one's own viewpoint. However, the brain mechanisms that control this process of automatically and effortlessly taking another's visual perspective have not yet been investigated.

To address these outstanding issues and further delineate the neural bases of simple visual perspective taking processes, the current study used the paradigm developed by Samson and colleagues (2010) to directly compare self and other perspective selection processes during fMRI. Participants were presented with pictures of a room with dots on the wall. Inside the room an avatar was positioned so that he or she would sometimes see all the dots visible to participants (consistent perspective) and sometimes be unable to see some of the dots visible to participants (inconsistent perspective). Hence, only on inconsistent trials did conflict arise between the participant's and the avatar's viewpoint; on consistent trials, the participant and the avatar could see the same number of dots. The basic assumption, supported by RT and error data, is that more demands are placed on selection processes in the inconsistent than consistent condition. A second experimental condition involved manipulating the target perspective. On "other" trials, participants were asked to judge how many dots the person in the room can see, whereas on "self" trials, participants were asked how many dots

they can see. Thus, for present purposes, the key feature of this paradigm is that neural processes involved in perspective selection for judgments of self and other can be directly compared.

Two central research questions can be distinguished. The first relates to whether the same brain areas are involved in perspective selection irrespective of which perspective has to be selected. ERP measurements of brain activity during a similar task suggest that the brain regions involved in perspective selection could be the same for self and other; lPFC was implicated in both forms of perspective selection (McCleery, Surtees, Graham, Richards, & Apperly, 2011). This finding suggests that the neural substrates involved in perspective selection processes may respond in a viewpoint-independent manner and rely on brain areas associated with inhibitory control, such as lPFC (van der Meer, Groenewold, Nolen, Pijnenborg, & Aleman, 2011; Samson et al., 2005; Vendrell et al., 1995). Alternatively, brain regions involved in perspective selection could be partially distinct for self and other, which prior ERP measurements would not have been able to capture because of spatial insensitivity (McCleery et al., 2011). For example, prefrontal regions that have been shown to orchestrate domain-general cognitive control could modulate activity "downstream" in a subset of brain regions specific to self and other representations (Miller & Cohen, 2001; Desimone & Duncan, 1995). Using fMRI, we will investigate if the processes involved in perspective selection are the same for self and other.

The second research question is based on prior behavioral findings (Samson et al., 2010), which suggest that on consistent trials judging another's perspective is less cognitively demanding than judging one's own. Hence, on consistent trials we predict that brain regions responsible for perspective selection will be engaged less during other-judgments than self-judgments. Findings consistent with this pattern would provide the first brain-based evidence for the claim that we not only automatically compute what other people see, but that we may compute this even before we are explicitly aware of our own perspective (Kovács et al., 2010; Samson et al., 2010).

METHODS

Participants

Eighteen right-handed participants from the University of Nottingham gave informed consent and participated in the study in exchange for a small inconvenience allowance. Ethical approval was gained through the Medical School Research Ethics Committee of the University of Nottingham. Two participants were later excluded from the study, one because of technical problems during scanning and the other for an abnormally high number of errors in the behavioral task (19% errors), leaving a total of 16 participants (three men, mean age = 22.4 years).

Task and Stimuli

The task was adapted for fMRI based on a prior behavioral paradigm (Samson et al., 2010; Experiment 1). Participants were presented with pictures of a room and asked to judge how many dots they (self-perspective) or a gender-matched computer-generated avatar (other-perspective) could see. On half of the trials, both participants and the avatar could see the same amount of dots (consistent perspective), whereas on the other half of trials, they saw a different amount of dots (inconsistent perspective). The judgment took the form of a verification task in which participants had to make a yes–no response as to whether the number of dots presented (ranging from 0 to 3) corresponded to the number of dots that the target person (self or avatar) could see (Figure 1 and Supplementary Figure S1). On half of the trials the number presented matched the perspective content to verify (i.e., a "yes" response), and on the other half of trials the number presented did not match the perspective content to verify (i.e., a "no" response). Responses were made on a scanner-compatible button box with the right hand. An index finger button press indicated "yes," whereas a middle finger button press indicated "no." On filler trials, there were no dots present in the room and participants
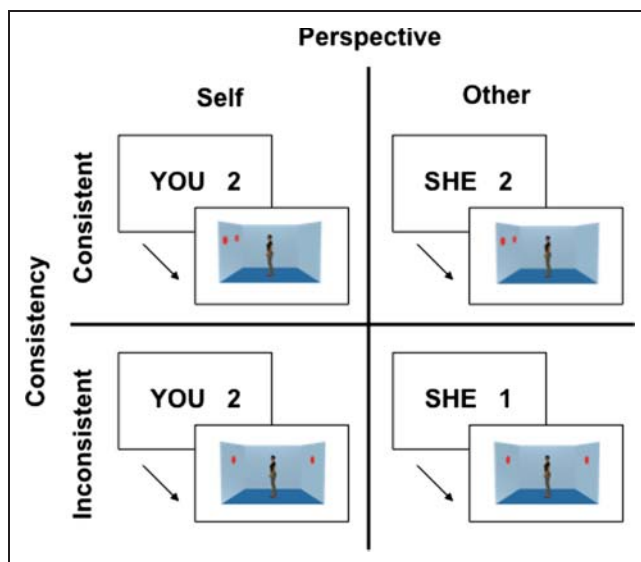
continued to indicate whether the number cue matched the amount of dots that the target person could see. Filler trials thus allowed the cued number "0" to also match self-perspective judgments.

A total of 152 trials (including eight filler trials) were spread evenly across the 2 (Consistency: consistent vs. inconsistent perspective) × 2 (Perspective: self vs. other) × 2 (Matching: matching vs. mismatching number) design. This produced four experimental conditions each for both matching and mismatching trials: Consistent Other, Consistent Self, Inconsistent Other, and Inconsistent Self. To yield an equal number of consistent and inconsistent perspective trials, consistent disc configurations were presented twice as often as inconsistent disc configurations (Supplementary Figure S1). In addition, the direction the avatar faced (left or right) was balanced across conditions.

Unlike the original behavioral study (Samson et al., 2010), the perspective and number cues were presented simultaneously rather than sequentially. Thus, each trial began with the presentation for 1000 msec of the perspective cue indicating which perspective participants had to judge ("YOU" or "S/HE") alongside the number cue indicating the amount of dots to verify (0–3). The two cues were presented horizontally next to each other in the center of the screen and in font Arial size 24. The picture of the room (640 × 480 pixels) was then immediately presented in the center of the screen for 1500 msec. Participants were instructed to respond as quickly and accurately as possible when the picture of the room appeared. The picture stayed on the screen until the 1500 msec had lapsed. Hence, the duration of each trial was 2500 msec including the presentation of text and picture. To introduce jitter, trials were interspersed by a variable ISI ranging between 6 and 16 sec and averaging 11 sec. During that ISI, a fixation cross appeared on the screen.

The 152 trials were divided into four runs of 38 trials with four or five trials per experimental condition. Each run lasted 8 min 50 sec and contained an equal number of self and other trials, consistent and inconsistent trials, and matching and mismatching trials (plus two filler trials). The order of the trials within a run was pseudorandomized to ensure that there were never two of the same ISI in a row, that the same picture was not shown twice in a row, and that each trial within a target experimental condition was preceded by different experimental conditions. The order of trials was then fixed within each run across subjects, but the order of presentation of the four runs was counterbalanced across participants. The stimuli were displayed using Presentation (Neurobehavioral Systems).

Figure 1. Experimental conditions and stimulus sequencing. Four conditions formed a 2 (Consistency: consistent vs. inconsistent) × 2 (Perspective: self and other) factorial design. The task for participants was to judge how many dots they (Self) or the avatar (Other) could see. The avatar and participant could either see the same (Consistent) or a different (Inconsistent) number of dots. Each trial commenced with the presentation of text, which specified the perspective from which to make a judgment from as well as the number of dots to verify. Subsequently, a picture was then presented that showed the avatar in a room. Participants had to verify (via a button press) if the number of dots was correct or incorrect according to the relevant perspective on that trial (self or other). Instructions were to respond as soon as possible after the picture was shown. The duration of each trial including text (1000 msec) and picture (1500 msec) was 2500 msec.

Image Acquisition

Scanning was performed in a 3T Philips Achieva scanner using an eight-channel-phased array head coil with 40 slices per repetition time (3 mm thickness), repetition time = 2500 msec, echo time = 35 msec, flip angle = 80°, field of view = 19.2 cm, matrix = 64 × 64. Each of the four

Figure 2. Behavioral data. (A) Mean RT. A Consistency × Perspective ANOVA showed there was a significant main effect of consistency with longer RTs for inconsistent than consistent trials. There was also a significant interaction between Consistency and Perspective. Post hoc *t* tests showed a greater difference between RTs (inconsistent > consistent) when participants

judged the other's perspective, although a marginally significant difference was also observed when judging their own perspective. Finally, whereas there was no significant difference between self- and other-perspective judgments on inconsistent trials (IO = IS), participants were quicker at judging the avatar's perspective than their own perspective on consistent trials (CS > CO). (B) Percentage error. The same Consistency × Perspective ANOVA performed on error rates showed only a significant effect of Consistency with more errors made on inconsistent than consistent trials. Error bars correspond to *SEM*. Abbreviations: C = consistent; I = inconsistent; O = other; S = self.
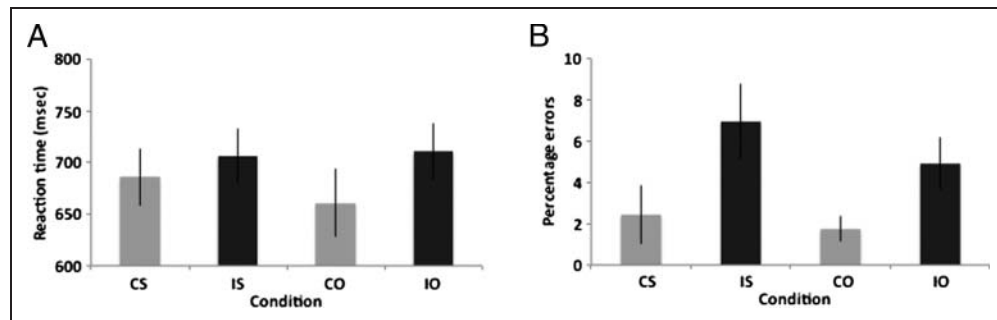
Data Analysis

Behavioral data were analyzed using SPSS (Version 18.0.0), and image analysis was performed in SPM8 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk/spm). Images were realigned, unwarped, corrected for slice timing, normalized to the Montreal Neurological Institute template with a resolution of 3 × 3 × 3 mm and spatially smoothed (8 mm). A design matrix was fitted for each participant with a total of 10 regressors per block, including one for the written cue period before each photograph, four each for both matching and mismatching trials (Consistent Other, Consistent Self, Inconsistent Other, Inconsistent Self), as well as one for Filler trials. In a second design matrix, an additional regressor was added, which included mean centered RT as a parametric variable according to the variable impulse model (Yarkoni, Barch, Gray, Conturo, & Braver, 2009; Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008). This second design matrix enabled comparison between results with and without the inclusion of RTs as a covariate (Yarkoni et al., 2009). Each trial was modeled as an event of no duration and convolved with the standard hemodynamic response function.

In line with the procedure of the original study (Samson et al., 2010), all mismatching trials were not analyzed further because of an imbalance in processing requirements. Specifically, mismatching consistent trials are the only trials where the cue does not correspond to any perspective; it is thus very easy to correctly reject the cue. On those trials, the ease of response is thus not solely determined by the consistency of the perspectives but also by the ease of cue verification. Thus, including mismatching trials in our analyses would inflate the consistency effect. To keep a balanced factorial design, we removed both mismatching consistent and mismatching inconsistent trials from further analysis. In addition, the cue period and Filler trials were not analyzed further. The remaining four conditions (Consistent Other, Consistent Self, Inconsistent Other, Inconsistent Self) comprised only "matching" trials and formed a 2 (Consistency: consistent vs. inconsistent) × 2 (Perspective: self vs. other) factorial design (Figure 1). During scanning, two behavioral variables were recorded: RT and accuracy. RT was calculated as the time between the appearance of the picture and the button press response, whereas accuracy was calculated in a binary fashion in terms of whether the verification response was correct or incorrect. RT and accuracy data were analyzed separately, each with a 2 (Consistency) × 2 (Perspective) repeated-measures ANOVA. Trials were removed from the design if participants did not respond (9 in total) and if a verification error was made (see Figure 2B) as atypical perspective selection processes may have been involved.

Our fMRI analyses centered around two research questions. First, we examined which brain regions are engaged in the process of selecting a perspective (self or other) when conflict exists between the one's own perspective and the perspective of the avatar (i.e., inconsistent trials). Thus, we compared the BOLD response during inconsistent trials with consistent trials for both self (Inconsistent Self > Consistent Self) and other conditions (Inconsistent Other > Consistent Other). The main effect of Consistency, collapsed across perspective, was also calculated in both directions (Inconsistent Other + Inconsistent Self > Consistent Other + Consistent Self, and its inverse).

Our second research question was motivated by the behavioral finding that, in consistent conditions, calculating the other's perspective (Consistent Other) is easier (as measured by RTs) than calculating one's own perspective (Consistent Self; Samson et al., 2010). Our analysis, therefore, compared consistent self trials with consistent other trials (Consistent Self > Consistent Other). The main effect of Perspective, collapsed across consistency, was also calculated in both directions (Consistent Self + Inconsistent

Self > Consistent Other + Inconsistent Other, and its inverse).

To further address our second research question, the interaction between Consistency and Perspective was calculated. Previous RT findings using the same task showed a Consistency × Perspective interaction: There was a greater difference between inconsistent and consistent conditions for other-perspective judgments than self-perspective judgments (Samson et al., 2010). Hence, the interaction tested for brain regions that showed a greater response for inconsistent compared with consistent conditions for other- than self-perspective judgments [(Inconsistent Other − Consistent Other) > (Inconsistent Self − Consistent Self)]. For completeness, the inverse interaction was also calculated [(Consistent Other − Inconsistent Other) > (Consistent Self − Inconsistent Self)].

Contrast images for all participants were taken to the second level for random effects analysis. For all second-level analyses, correction for multiple comparisons was performed at the cluster level (Friston, Worsley, Frackowiak, Mazziotta, & Evans, 1994), using a voxel-level threshold of $p < .005$ and 40 voxels and a family-wise error (FWE) cluster-level correction of $p < .05$. For each contrast, brain regions surviving the voxel-level threshold are reported in tables, and regions surviving the FWE cluster correction are highlighted in bold font. Brain regions were localized using a human brain atlas (Duvernoy, 1999) in combination with an on-line search tool (sumsdb.wustl.edu/sums/) and the SPM Anatomy toolbox (Eickhoff et al., 2005).

To test the hypothesis that there could be common cognitive and neural processes involved in perspective selection during judgments of self and other, we searched for overlapping patterns of activity between independent contrasts. This conjunction method requires that all comparisons in the conjunction are individually significant (Nichols, Brett, Andersson, Wager, & Poline, 2005) at our designated threshold ($p < .005, K = 40$). For the purpose of illustration, parameter estimates were extracted from a 10-mm radius sphere focused on areas of overlap between contrasts.

RESULTS

Behavioral Data

RT

The Consistency × Perspective ANOVA showed a main effect of Consistency, $F(1, 15) = 18.67, p < .01, \eta p^2 = 0.554$, with longer RTs in the inconsistent than the consistent condition (Figure 2A). There was no main effect of Perspective, $F(1, 15) = 1.30, p = .27, \eta p^2 = 0.080$, with participants judging equally fast their own and the avatar's perspective, but there was a significant Consistency × Perspective interaction effect, $F(1, 15) = 7.01, p < .05, \eta p^2 = 0.319$. Post hoc t tests showed a greater difference between RTs (inconsistent > consistent) when participants judged the other's perspective (IO > CO,

$t(15) = 4.55, p < .001$), although a marginally significant difference was also observed when judging their own perspective (IS > CS, $t(15) = 2.11, p = .05$; Figure 2A). In addition, consistent with the original behavioral findings (Samson et al., 2010), whereas there was no significant difference between self- and other-perspective judgments on inconsistent trials (IO = IS, $t(15) < 1$), participants were quicker at judging the avatar's perspective than their own perspective on consistent trials (CO < CS, although the difference was marginally significant, $t(15) = 1.97, p = .07$; Figure 2A).

Errors

The same Consistency × Perspective ANOVA performed on error rates showed a significant effect of Consistency, $F(1, 15) = 17.07, p < .01, \eta p^2 = 0.532$, with more errors made on inconsistent than consistent trials (Figure 2B). However, there was no main effect of Perspective or a Consistency × Perspective interaction effect (both $Fs < 1$). On the basis of this pattern of error rates, the profile observed in RT cannot be accounted for by a speed–accuracy trade-off.

fMRI Data

To identify the brain areas engaged during the selection of one's own perspective as well as the selection of someone else's perspective, we looked for brain regions that showed a greater BOLD response for inconsistent compared with consistent trials. When judging the avatar's perspective, left dorsolateral prefrontal cortex (dlPFC) as well as bilateral posterior parietal cortices showed a greater response for inconsistent than consistent trials at the whole-brain cluster-corrected threshold (Inconsistent Other > Consistent Other; Table 1A). When judging one's own perspective, no brain regions showed a greater response for inconsistent compared with consistent trials at the whole-brain cluster-corrected threshold (Inconsistent Self > Consistent Self). Two regions of cingulate cortex did survive the uncorrected threshold (Table 2A), but neither of these overlapped with brain regions identified in the Inconsistent Other > Consistent Other contrast. Although not directly relevant to our primary research questions, for completeness the results of the main effect of consistency (collapsed across self and other trials) are reported in Supplementary Table S1.

To address our second research question, which focused on why RTs for other-perspective judgments are facilitated on consistent trials compared with self-perspective judgments, we considered brain regions that showed a greater response for Consistent Self compared with Consistent Other trials. Right dlPFC and right pIPS extending into angular gyrus showed this pattern of response at the whole-brain cluster-corrected threshold. Several brain regions showed the same pattern at the uncorrected threshold, including left dlPFC, left pIPS, and left TPJ (Table 1B).

Table 1. Brain Regions Showing Inconsistent Other (IO) > Consistent Other (CO), Consistent Self (CS) > Consistent Other (CO), and Inconsistent Self (IS) > Consistent Other (CO)

Region	Number of Voxels	T	p Cluster Corrected (FWE)	x	y	z
A) IO > CO						
Left posterior IFG extending into MFG (dlPFC)	**400**	**5.82**	**<.01**	**−48**	**20**	**22**
				−45	**14**	**49**
				−54	**29**	**22**
Left anterior IFG/lateral orbital gyrus	69	5.47	.614	−45	41	−11
Left posterior ITG	64	5.28	.669	−54	−49	−11
				−60	−43	−14
				−63	−55	−11
Right posterior ITG	106	5.23	.293	66	−43	−11
				57	−55	−17
				66	−34	−11
Right posterior IPS extending into IPL (angular gyrus)	**328**	**5.17**	**<.01**	**36**	**−64**	**40**
				42	**−40**	**28**
				33	**−67**	**58**
Left IPL (angular gyrus) and TPJ extending into posterior IPS	**384**	**4.83**	**<.01**	**−51**	**−55**	**37**
				−36	**−70**	**49**
				−36	**−61**	**55**
Right posterior IFG	150	4.73	.113	48	17	34
				36	20	31
				33	5	31
Right posterior MFG/SFS (dlPFC)	42	4.65	.895	33	11	58
B) CS > CO						
Left anterior STG	74	6.74	.494	−51	−13	−2
				−48	−25	7
Right posterior MFG extending into SFG (dlPFC)	**204**	**5.52**	**<.05**	**33**	**17**	**58**
				21	**35**	**55**
				27	**26**	**58**
Right MFG/PMd	77	4.91	.462	42	2	49
				45	17	49
				51	11	43
Right thalamus	77	4.81	.462	21	−13	4
				12	−16	4
				30	−19	7
Right IPL (angular gyrus) extending into TPJ	**260**	**4.72**	**<.01**	**54**	**−55**	**28**
				51	**−58**	**40**
				45	**−49**	**28**

Montreal Neurological Institute Coordinates

Table 1. (*continued*)

Region	Number of Voxels	T	p Cluster Corrected (FWE)	Montreal Neurological Institute Coordinates		
				x	y	z
Left IPL (angular gyrus) extending into TPJ	115	4.57	.186	−51	−58	25
				−54	−55	43
Left anterior IFG/STG	61	4.45	.647	−45	14	−5
Right posterior ITG	75	4.36	.484	63	−25	−11
				63	−43	−14
				54	−49	−11
Left posterior IPS	79	4.36	.442	−33	−67	43
Right anterior IFG/STG	126	4.21	.142	54	11	−5
				57	17	7
Left MFG/PMd	125	4.04	.145	−39	8	58
				−42	−7	58
				−39	5	49
Right fusiform gyrus	45	3.79	.841	30	−70	−8
				21	−70	1
Right medial SPL/precuneus	144	3.53	.091	6	−79	49
				6	−67	61
				−3	−70	34
Left MFG (dlPFC)	47	3.37	.819	−45	11	34
				−45	10	34
				−42	17	46
C) IS > CO						
Bilateral anterior thalamus	129	6.88	.093	12	−7	4
				−15	−4	4
				−3	−10	−2
Left IPL (angular gyrus), TPJ, and posterior IPS	**1908**	**6.84**	**<.01**	**−42**	**−55**	**34**
				−33	**−64**	**46**
				−51	**−46**	**43**
Left middle orbital gyrus extending into IFG and MFG (dlPFC)	**306**	**5.93**	**<.01**	**−30**	**47**	**−5**
				−30	**23**	**19**
				−42	**38**	**25**
Left posterior MFG extending into medial SFG dorsal precentral gyrus	**318**	**5.29**	**<.01**	**−27**	**17**	**61**
				−39	**−4**	**61**
				−30	**2**	**58**
Right posterior SFG extending into MFG and dorsal precentral gyrus	**295**	**5.27**	**<.01**	**24**	**11**	**67**
				39	**20**	**34**
				33	**5**	**52**

Table 1. (*continued*)

Region	Number of Voxels	T	p Cluster Corrected (FWE)	Montreal Neurological Institute Coordinates		
				x	y	z
Left cerebellum	120	5.21	.119	**−33**	**−70**	**−32**
				−33	**−55**	**−35**
				−33	**−46**	**−41**
Right cerebellum	**325**	**4.94**	**<.01**	30	−79	−32
				15	−79	−32
				3	−79	−29
Left posterior ITG	**168**	**4.36**	**<.05**	**−51**	**−43**	**−11**
				−57	**−46**	**7**
				−63	**−58**	**−8**
Left posterior thalamus	78	4.24	.381	−3	−22	13
				−12	−40	7
				−18	−25	13

Only regions surviving a voxel-level threshold of $p < .005$ uncorrected and 40 voxels are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed.

Bold indicates regions that survive the FWE cluster-corrected threshold at $p < .05$.

I/M/S FG = inferior/middle/superior frontal gyrus; I/M/S TG = inferior/middle/superior temporal gyrus; I/S PL = inferior/superior parietal lobule; IPS = intraparietal sulcus; mPFC = medial prefrontal cortex.

Table 2. Brain Regions Showing Inconsistent Self (IS) > Consistent Self (CS), Inconsistent Other (IO) > Inconsistent Self (IS), Inconsistent Self (IS) > Inconsistent Other (IO)

Region	Number of Voxels	T	p Cluster Corrected (FWE)	Montreal Neurological Institute Coordinates		
				x	y	z
A) IS > CS						
Rostral ACC	57	5.35	.762	3	23	7
Right middle cingulate cortex	73	5.03	.594	21	−16	34
				24	−31	34
				21	−16	43
B) IO > IS						
No suprathreshold clusters						
C) IS > IO						
Right posterior hippocampus	44	4.21	.857	27	−37	−2
Left fusiform gyrus extending into lingual gyrus	83	3.99	.415	−30	−67	−5
				−21	−55	4
				−15	−70	7

Only regions surviving a voxel-level threshold of $p < .005$ uncorrected and 40 voxels are reported. Subpeaks more than 8 mm from the main peak in each cluster are listed.

Abbreviations as in Table 1.

These bilateral frontoparietal clusters overlapped with those produced by the contrast Inconsistent Other > Consistent Other (Figure 3). Again for completeness, the results of the main effect of perspective (collapsed across inconsistent and consistent trials) are reported in Supplementary Table S2.

Two clear findings emerge from these analyses: (1) Inconsistent Other and Consistent Self activate a common set of brain regions spanning frontoparietal cortex more than Consistent Other (Figure 3) and (2) Inconsistent Self does not engage these same frontoparietal brain regions more than Consistent Self (Table 2A). Next we examined if Inconsistent Self activates regions of frontoparietal cortex more than Consistent Other (Inconsistent Self > Consistent Other). Bilateral pIPS extending into angular gyrus as well as bilateral dlPFC showed a greater response for Inconsistent Self than Consistent Other at the whole-brain cluster corrected threshold (Table 1C). Overlap analysis of three contrasts (Inconsistent Other > Consistent Other, Consistent Self > Consistent Other and Inconsistent Self >

Consistent Other) confirmed that the same regions of frontoparietal cortex were engaged for all three contrasts at our designated voxel-wise threshold ($p < .005$, $K = 40$; Figure 3). If the more conservative whole-brain cluster-corrected threshold was used for all contrasts ($p < .05$ FWE), overlap only remained in right angular gyrus.

Consistent with prior RT findings (Samson et al., 2010), we also calculated the interaction between consistency and perspective, which tests for brain regions that show a greater difference between inconsistent than consistent trials for other than self-judgments [(Inconsistent Other − Consistent Other) > (Inconsistent Self − Consistent Self)]. Right pIPS extending into angular gyrus showed this pattern of response (Supplementary Table S3). In an exploratory analysis, we lowered the number of contiguous voxels necessary to pass our threshold from 40 to 10, and we observed responses bilaterally in dlPFC, which overlapped with the results of our conjunction analysis (Supplementary Table S3). The inverse interaction showed no responses.

Figure 3. Overlap between contrasts. Three contrasts are displayed, each of which involves a comparison with the consistent-other condition: (1) inconsistent-other (red); (2) consistent-self (green); and (3) inconsistent-self (blue). Overlap between all three contrasts is displayed in white. Plotted are parameter estimates (SPM betas) that were extracted from 10-mm radius spheres focused on regions that show overlap between all three contrasts. In cases of bilateral responses, only the left hemisphere response is plotted. Contrasts are displayed using a $p < .005$, $K = 40$ voxel-wise threshold. Abbreviations: C = consistent; I = inconsistent; O = other; S = self.
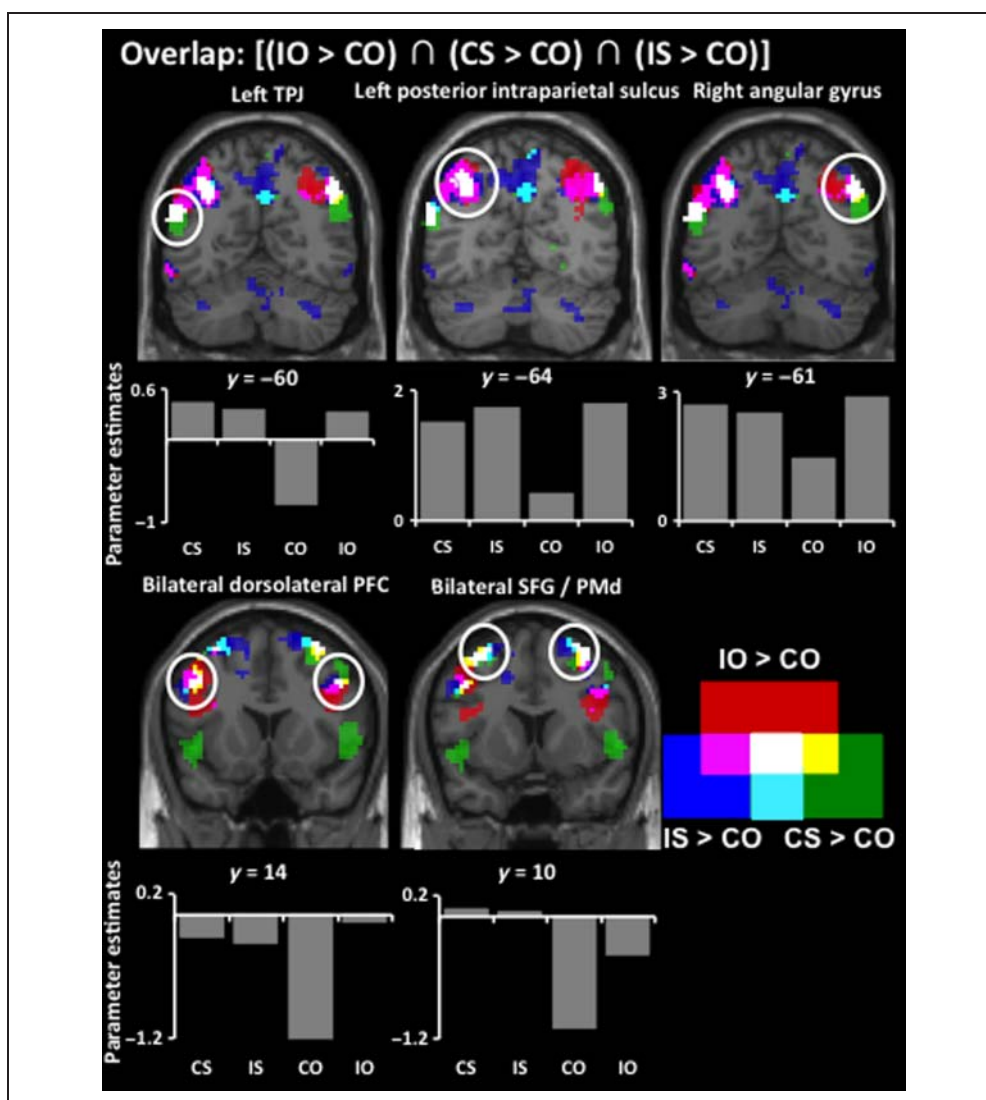
Importantly, when RT was included as an additional regressor in a second design matrix according to the variable impulse model (Yarkoni et al., 2009; Grinband et al., 2008), the results were almost identical. Because the results were unaffected when we accounted for the influence of "time-on-task" effects, we do not report results from this additional analysis.

DISCUSSION

The current fMRI study used a behavioral paradigm that required participants to select between competing visual perspectives (Samson et al., 2010). We provide two main extensions to current knowledge. First, we demonstrate that brain regions within dlPFC and posterior parietal cortex respond in a viewpoint-independent manner to select a task-relevant over a task-irrelevant perspective. More specifically, following the computation of two competing visual perspectives, common regions of frontoparietal cortex are engaged to select one's own viewpoint over another as well as select another's viewpoint over one's own. Second, in the absence of conflict between the content of competing perspectives, we showed a reduced engagement of frontoparietal cortex when judging another's visual perspective relative to one's own. This latter finding provides the first brain-based evidence for the hypothesis that, in some situations, another person's perspective is automatically and easily computed and thus less cognitive control is required to select it over one's own perspective. Thus, we provide stronger evidence for the claim that we not only automatically compute what other people see, but that we compute this even before we are explicitly aware of our own perspective. We discuss each of these findings in turn as well as outline broader implications for understanding the cognitive and neural bases of ToM.

Common Neural Substrates for Selecting between Perspectives of Self and Other

Prior behavioral research has suggested that selecting a target perspective could involve a common cognitive process, which operates in a viewpoint-independent manner (Qureshi et al., 2010; Samson et al., 2010). We extend these findings by demonstrating that the neural regions engaged during perspective selection also exhibit viewpoint-independence. Specifically, regions of frontoparietal cortex, including dlPFC, pIPS, angular gyrus, and TPJ, are engaged to select the other's viewpoint over one's own as well as select one's own viewpoint over another person's viewpoint. Prior fMRI studies have shown similar dlPFC and parietal responses for other compared with self-perspective judgments (Schnell et al., 2011; David et al., 2006, 2008; Aichhorn et al., 2006; Vogeley et al., 2004). The results of the current study extend prior findings to show that the response in lateral frontoparietal cortex may not be specific to other-perspective processing, but instead these regions may be involved more generally in perspective selection, including both other- and self-perspective selection.

A common neural response for selection of self and other visual perspectives concurs with a broad literature, which suggests that the representation of self and other may rely on a partially shared cognitive and neural architecture (Zaki & Ochsner, 2011). Here, however, it is not the content of the cognitive or neural representation that is shared between self and other like the majority of previous studies (i.e., emotion, sensation, action, belief; Keysers & Gazzola, 2009; Decety & Grèzes, 2006), but it is the process of selecting or prioritizing a target perspective that is shared. This suggests that shared representations are not restricted to mental state content but also include a shared process of selection, specifically perspective selection.

Through the use of fMRI, we have been able to demonstrate that perspective selection engages a distributed set of frontoparietal brain regions. Prior ERP work implicated lPFC in the process of perspective selection for self as well as other judgments (McCleery et al., 2011). Prefrontal cortex has been frequently associated with inhibitory control (Vendrell et al., 1995) and specifically self-inhibition during ToM judgments of others (Hartwright, Apperly, & Hansen, 2012; Rothmayr et al., 2011; Shibata & Inui, 2011; van der Meer et al., 2011; Samson et al., 2005; Vogeley et al., 2001). As such, we suggest that perspective selection is partly achieved through engagement of dlPFC during the inhibition of task-irrelevant perspectives. Rather than solely relying on lateral frontal brain regions, we show the additional involvement of ventral and dorsal lateral parietal cortex in perspective selection. The involvement of parietal cortex could reflect inhibitory control (see next section for further discussion), which complements inhibitory mechanisms sustained in frontal cortex. However, parietal cortex involvement in perspective selection, specifically angular gyrus and TPJ, is also compatible with the proposal that these areas sustain a self-other discrimination (Jeannerod, 2004; Decety & Sommerville, 2003), which is enhanced when selecting between conflicting perspective contents (Shibata & Inui, 2011; Corradi-Dell'Acqua et al., 2008; David et al., 2006, 2008; Aichhorn et al., 2006; Vogeley et al., 2004). Accordingly, the process of perspective selection may involve a cognitive and neural architecture that extends beyond inhibitory control mechanisms alone (see Figure 4). Further delineation of the processes involved in perspective selection is an important direction for future research.

Automatic Computation of Other People's Perspectives

One unexpected finding in the original behavioral experiments (Samson et al., 2010), but which we replicated here, is that in some situations, another person's viewpoint is more salient than one's own viewpoint. Here we add
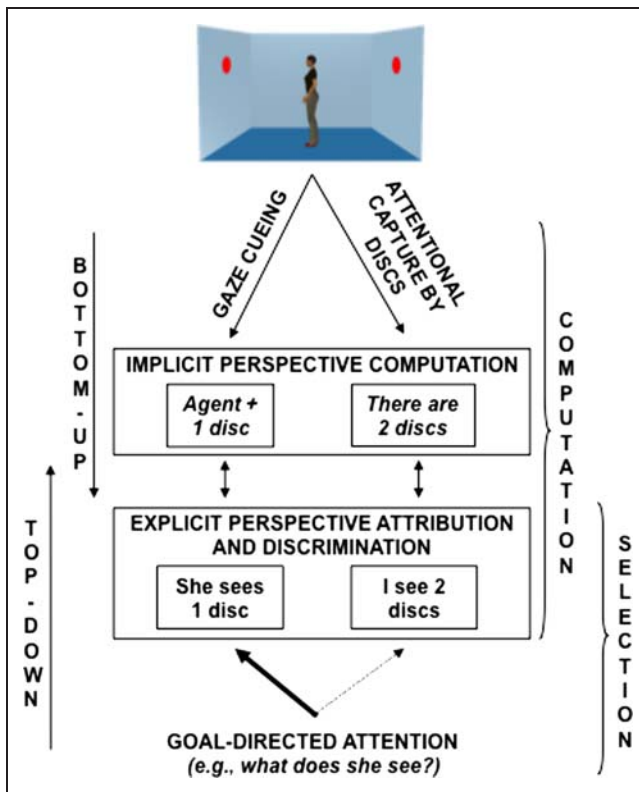
Figure 4. Schematic representation of the hypothesized processes involved in visual perspective taking as discussed in Samson et al. (2010). Perspective computation would be partly achieved via bottom–up (scene-driven) processes, such as the avatar's gaze direction and attentional capture by the red discs. These bottom–up processes would occur automatically on seeing the scene ("implicit perspective computation"). A further set of processes would be required to attribute a perspective content to self as well as other and also keep clear the distinction between the two perspectives ("explicit perspective attribution and discrimination"). Processes of attribution and discrimination would be involved in both the computation and selection of the relevant perspective. Perspective selection would also be achieved via top–down (instruction-driven) processes, which bias attention to the task-relevant perspective. It is proposed that perspective selection processes involve a combination of inhibitory and reinforcing signals that together produce a priority map determining which perspective to use. In addition, the extent to which perspective selection processes are recruited would depend on the salience of the task-irrelevant perspective. The current study shows that these selection processes engage a frontoparietal set of brain regions.

brain-based evidence for a similar conclusion. Specifically, when there is no discrepancy in the content of viewpoint between self and other, regions of frontoparietal cortex are engaged more when judging one's own rather than another's perspective. This suggests that the other's perspective is calculated even before we explicitly construe our visual experience (i.e., the scene we see) as being our own perspective. Consequently, when judging the other person's point of view, there is less perspective competition and fewer demands placed on perspective selection processes than selecting one's own perspective (Samson et al., 2010). Put another way, when judging

one's own point of view, one has to orient attention away from the more salient other-perspective, which places a greater demand on the cognitive resources involved in perspective selection. Furthermore, we demonstrate that in the absence of conflict between the content of visual perspectives the same brain regions are involved in the process of selecting a target perspective as when viewpoints are discrepant (i.e., lPFC, pIPS, angular gyrus, and TPJ). This suggests that frontoparietal cortex is engaged to select target perspectives independent of whether the content of viewpoints agree or conflict. Although we would predict a partially distinct set of brain regions to be engaged during processes of perspective computation compared with selection, we are unable to test this hypothesis using the current paradigm. The current study was not designed to probe the brain regions that are involved in the computation of perspectives; it instead focused on perspective selection. We therefore encourage future research to test how processes of perspective computation and selection interact within both cognitive and neural architectures.

These results converge on a neurocognitive account of information encoding that extends beyond the notion that one's own perspective primarily serves as the default viewpoint (Shelton & McNamara, 1997, 2001), which is then used to calculate another's perspective (Epley et al., 2004). Rather, depending on the social context, either one's own viewpoint is more salient and hence additional cognitive and neural resources can be required to consider another's viewpoint (Keysar et al., 2003; Kessler & Thomson, 2010) or another's viewpoint is more salient and extra cognitive and neural resources can be required to consider one's own viewpoint (Samson et al., 2010). Together, these findings suggest that ToM judgments can initially be biased toward one's own or another's viewpoint depending on situational demands (Samson & Apperly, 2010).

This proposal is consistent with the view that multiple perspectives can be "readied" in parallel with perspective selection occurring through an interplay of top–down and bottom–up biases (Samson, 2009; see also Figure 4). Previous research investigating visual salience has implicated left IPS in the process of selecting a low-salience visual feature while ignoring a high-salience distractor (Mevorach, Shalev, Allen, & Humphreys, 2009; Mevorach, Humphreys, & Shalev, 2006). Moreover, left IPS has been shown to suppress neural responses in a region of occipital cortex that typically responds to salient visual cues (Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010). Similar top–down regulation of salient bottom–up visual features could provide an account of the present response in pIPS. That is, the avatar's bodily orientation and gaze direction, which are coded in posterior STS (Allison, Puce, & McCarthy, 2000), could have provided a visual cue that made the avatar's perspective more salient than the self-perspective. Consequently, when making a self-judgment, pIPS may provide top–down control to suppress this bottom–up bias to reorient to one's own viewpoint. Future research may

develop models of perspective taking that are based upon "biased competition" within distributed but interacting neuronal populations in a similar manner to recent accounts of attention (Beck & Kastner, 2009; Itti & Koch, 2000) and action selection (Cisek & Kalaska, 2010). These models should include both perspective computation and selection processes.

So far, we have discussed how the relative salience between self- and other-perspectives may influence the demands of perspective selection. It is also important to consider how other factors can influence the demands of perspective selection such as whether the context affords explicit perspective judgments. In the current paradigm, participants were explicitly asked to verify perspective contents, a situation that loads particularly high on perspective selection (our process of interest). The extent that perspective selection processes are required in other social contexts, which involve less explicit perspective judgments, is an important question for future research.

Conclusion

To successfully guide social behavior, it is important to keep track of what you and other people see, believe, or desire, as well as to be able to flexibly switch between such perspectives of self and other. We demonstrate that lateral frontoparietal brain areas sustain perspective selection processes in a viewpoint-independent manner. In other words, common frontoparietal brain areas select the other's viewpoint over one's own as well as select one's own viewpoint over another person's viewpoint. We also found a reduced engagement of frontoparietal cortex when judging another's visual perspective relative to one's own. This latter finding provides the first brain-based evidence for the hypothesis that, in some situations, another person's perspective is automatically and effortlessly computed and thus less cognitive control is required to select it over one's own perspective. Together, our findings suggest that dlPFC, pIPS, angular gyrus, and TPJ are set of brain regions that are flexibly recruited depending on the social task. More specifically, the relative salience of competing (visual) perspectives may be one factor that determines how much these regions are recruited during ToM judgments.

Acknowledgments

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