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Developmental Differences in the Control of Action Selection by Social Information

Iroise Dumontheil^{1*}, Hauke Hillebrandt^{1*}, Ian A. Apperly²,
and Sarah-Jayne Blakemore¹

Abstract

■ Our everyday actions are often performed in the context of a social interaction. We previously showed that, in adults, selecting an action on the basis of either social or symbolic cues was associated with activations in the fronto-parietal cognitive control network, whereas the presence and use of social versus symbolic cues was in addition associated with activations in the temporal and medial prefrontal cortex (MPFC) social brain network. Here we investigated developmental changes in these two networks. Fourteen adults (21–30 years of age) and 14 adolescents (11–16 years) followed instructions to move objects in a set of shelves. Interpretation of the instructions was conditional on the point of view of a visible “director” or the meaning of a symbolic cue (Director Present vs. Director Absent) and the number of potential referent objects in the shelves (3-object vs. 1-object). 3-object

trials elicited increased fronto-parietal and temporal activations, with greater left lateral prefrontal cortex and parietal activations in adults than adolescents. Social versus symbolic information led to activations in superior dorsal MPFC, precuneus, and along the superior/middle temporal sulci. Both dorsal MPFC and left temporal clusters exhibited a Director × Object interaction, with greater activation when participants needed to consider the directors’ viewpoints. This effect differed with age in dorsal MPFC. Adolescents showed greater activation whenever social information was present, whereas adults showed greater activation only when the directors’ viewpoints were relevant to task performance. This study thus shows developmental differences in domain-general and domain-specific PFC activations associated with action selection in a social interaction context. ■

INTRODUCTION

How is an appropriate action selected among many possibilities? How do we decide to pick a particular fruit out of many on offer at the supermarket? The PFC is thought to support the integration of information from the current environment (the smell, color, appearance, and identity of melons on stand) and internal information generated more or less remotely in time (the plan to invite friends for dinner, the decision to have melon as a starter, but also the value associated with melons compared with other fruits); to orient attention appropriately (toward the stand and the most appetizing looking melon); and to select an action appropriate with the current goals (picking up the selected melon; e.g., Burgess, Gilbert, & Dumontheil, 2007; Koechlin & Summerfield, 2007; Fuster, 2000; Baron-Cohen, Leslie, & Frith, 1986). Using visual search paradigms, previous research has investigated the selection of targets combining different properties in arrays of simple stimuli (Humphreys, Allen, & Mavritsaki, 2009; Davis & Palmer, 2004; Booth et al., 2003). Results suggest a dissociation between bottom-up (spontaneous orientation toward a stimulus) and top-down (intentionally driven by knowledge, expectations, and goals) processes of visuospatial

selective attention (Beck & Kastner, 2009; Hahn, Ross, & Stein, 2006). However, few studies have attempted to use more complex stimuli.

A large number of our everyday actions are performed in a social interactive context. If you are paying at a shop checkout, you need to perform a series of actions that ensures the shopkeeper knows whether you wish to pay by cash or credit card, and so on. These interactions are sometimes based on verbal communication and, at other points, on communicative gestures. For example, making sure the shopkeeper can see you have taken your credit card out of your wallet informs the shopkeeper that you want to pay by card. This type of interaction relies on an understanding of other people’s mental states, also called theory of mind or mentalizing (Frith & Frith, 2007). Thus, we often need to use the theory of mind to make top-down decisions and select actions that are appropriate to the inferred mental state of the people we interact with in complex real-world situations. The combination of domain-general processes supporting selective attention, action selection and cognitive control, and cognitive processes that may be specific to social information and mentalizing, is the focus of this study. PFC is involved in both top-down action selection (Burgess et al., 2007) and mentalizing (Frith & Frith, 2007), in particular, in ill-structured or novel situations (Apperly, 2011). Following previous

¹University College London, ²University of Birmingham

*Contributed equally to this work.

work in adults (Dumontheil, Küster, Apperly, & Blakemore, 2010), the aim of the current study was to investigate the development of these domain-general and domain-specific processes during adolescence, using fMRI and a paradigm that permits the comparison of action selection in a social versus nonsocial context.

Adolescence is a period of social and psychological development during which social awareness and behavior undergo profound change (Brown, 2004; Eisenberg & Morris, 2004). At the same time, higher cognitive control and reasoning abilities mature both in terms of behavior and brain function (Dumontheil & Blakemore, 2012; Crone & Ridderinkhof, 2010; Luna, Padmanabhan, & O'Hearn, 2010; Crone, 2009). As well as alterations in hormone levels and social environment, a possible cause of these developmental changes are structural changes taking place in brain areas involved in social cognition, including the medial PFC (MPFC), the superior temporal cortex, and the TPJ (Saxe, 2006; Frith & Frith, 2003; Gallagher & Frith, 2003), and in brain regions involved in cognitive control tasks, in particular, lateral parts of PFC. Notably, frontal and temporal lobes undergo protracted structural development in humans (Shaw et al., 2008; Gogtay et al., 2004; Giedd et al., 1999; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999). Developmental functional imaging studies of mental state attribution have consistently shown that the MPFC activity during a variety of mentalizing tasks (e.g., understanding irony or thinking about one's intentions) decreases between adolescence and adulthood (see Burnett, Sebastian, Cohen-Kadosh, & Blakemore, 2011; Blakemore, 2008, for review). In addition, there is evidence of developmental changes in functional connectivity between MPFC and other parts of the mentalizing network during adolescence (Burnett & Blakemore, 2009). The age-related changes lie in the part of the MPFC superior to $z = 0$ labeled anterior rostral medial frontal cortex (MFC), which is recruited by tasks involving self-knowledge, person perception, and mentalizing, in contrast to a more ventral "orbital MFC" region and a more posterior "posterior rostral MFC" region (Amodio & Frith, 2006). Other groups use slightly different subdivisions of the MPFC, with a more superior border at $z = 20$ (Van Overwalle, 2009) to distinguish between "ventral MPFC" and "dorsal MPFC." This dissociation has been related to a distinction between mentalizing judgments made toward the self or similar others versus on dissimilar others (Tamir & Mitchell, 2010; Van Overwalle, 2009; Jenkins, Macrae, & Mitchell, 2008; Mitchell, Macrae, & Banaji, 2006). The developmental cognitive control literature has shown less consistent findings, with studies showing both decreases and increases in lateral PFC activations as well as qualitative changes with age during adolescence (see Crone & Ridderinkhof, 2010; Luna et al., 2010; Astle & Scerif, 2009; Casey, Jones, & Hare, 2008; Bunge & Wright, 2007).

The ability to infer mental states, or mentalizing, develops in a step-wise fashion during the first 5 years of life (Frith & Frith, 2003) at which point children are able to

reason explicitly about theory of mind. However, this ability does not always lead to an automatic, on-line use of theory of mind information even in adolescents and adults. For instance, Keysar and colleagues (Keysar, Lin, & Barr, 2003; Keysar, Barr, Balin, & Brauner, 2000) designed a task in which participants were faced with a set of shelves containing objects that were either visible or not visible from the viewpoint of a "Director" (a confederate). The director asked participants to move objects in the shelves, and critical instructions required participants to use information about the director's viewpoint to correctly interpret their instructions. In this Director task, adults did not reliably use their theory of mind knowledge to interpret the intentions of others (Keysar et al., 2000, 2003). Around 50% of the time, they failed to use information about the director's perspective and instead erroneously used their own (egocentric) viewpoint only when trying to follow the director's instruction. These results were replicated using a computerized version of the paradigm and controlling for the inhibitory control demands of the task with a matched no-director condition (Apperly et al., 2010). We have further found that egocentric errors in this task are accentuated in adolescence, with an even stronger egocentric bias observed in 14- to 17-year-old adolescents than in young adults (Dumontheil, Apperly, & Blakemore, 2010). These results suggest that the ability to take another person's perspective to select appropriate actions is still undergoing development at this relatively late stage. The Director task differs from other theory of mind tasks in that it requires participants to have a functioning theory of mind, to compute the perspective and intentions of another person (the director), and use this theory of mind information in concert with other cognitive processes such as executive functions to overcome their egocentric bias and select the appropriate response quickly and accurately (Apperly et al., 2010). It is proposed that it is this interaction between theory of mind and executive functions that continues to develop in late adolescence and is still prone to errors in adults (see Dumontheil, Apperly, et al., 2010).

In the current study, we adapted a computerized version of the Director task (Apperly et al., 2010; Dumontheil, Apperly, et al., 2010) for fMRI (Dumontheil, Küster, et al., 2010). Whereas the previous studies using this paradigm were designed to probe the use of social cues (perspective taking) in a natural way via assessing differential error rates (which are naturally quite high as described above), the present version included extensive task instructions and practice to minimize error rates and compare fMRI data across groups performing at consistently high levels of accuracy. Our goal was to use this task variant to assess the development between adolescence and adulthood of the neural substrates associated with (1) the selection of an appropriate action in the context of alternative options proposed in a complex stimulus; (2) the presence of social information versus symbolic cues as part of the stimuli; and (3) the use of social cues as opposed to symbolic cues

for the selection of the appropriate action from the alternative options. Note that, although beyond the scope of the current study, the computation of the value of different objects or actions may be another important aspect of action selection and may be affected by personal and social factors developing during adolescence.

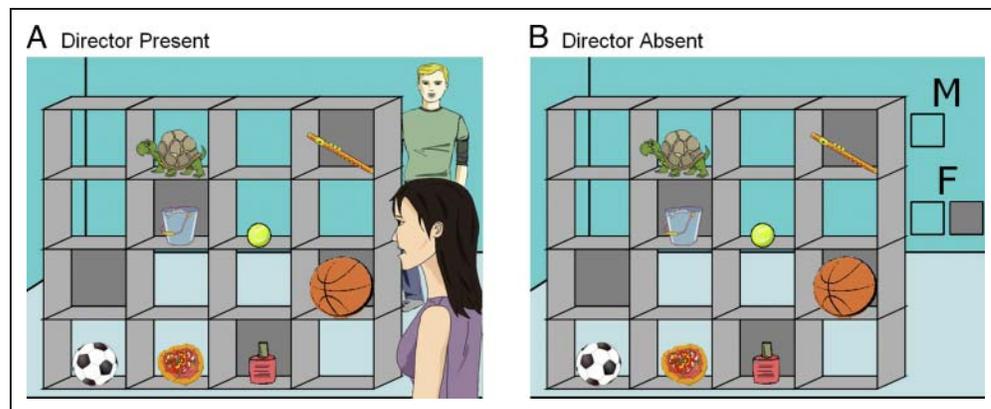
If mentalizing is a specialized and domain-specific cognitive process (e.g., Leslie, 2005; Sperber & Wilson, 2002; Stone, Baron-Cohen, & Knight, 1998; see Apperly, 2011, for discussion), then we might expect differential performance and the recruitment of regions of the social brain network (Frith & Frith, 2007; Brothers, 1990) when the guiding information is of social nature compared with more arbitrary symbolic stimuli. This social stimuli condition might thus recruit both domain-general action selection resources and domain-specific resources that are involved in processing social information and mentalizing. Such a pattern has previously been observed in adults, with nonoverlapping brain regions implicated in response selection and belief attribution during a belief attribution task (Saxe, Schulz, & Jiang, 2006; see also Saxe, Carey, & Kanwisher, 2004).

Participants followed auditory instructions to move objects in a set of shelves. A 2×2 factorial design with the factors Director (Director Present vs. Director Absent) and Object (3-object vs. 1-object) was employed. In the Director Present condition, two directors were shown on the display, one female and one male. One of them stood behind the shelves, facing the participant, whereas the other stood on the same side of the shelves as the participant. In the 3-object condition, participants needed to use the social cues, that is, the position of the speaking director, to select and move the appropriate object (see Figure 1A). The instructions in these blocks referred to an object that was one of three exemplars in the shelves (the ball). Two of these objects could correspond to the heard instruction (“Move the large ball up”) de-

pending on the director’s viewpoint. The largest ball (or equivalent) was always located in a closed shelf (not visible from the back), whereas the second largest ball was located in an open shelf. Importantly, when considering the identity of the director (male voice), only one of the objects was the appropriate response (the football); the other object corresponded to the other viewpoint and was thus a distractor (the basketball). The third object was another type of distractor that did not fit any of the perspectives (the tennis ball). On half of the Director Present 3-object trials, the perspective of the director issuing the instruction was different from that of the participant; on the other half, the director’s and participant’s perspectives were the same. This varied on a trial-by-trial basis; thus, participants needed to take into account the director’s perspective on every trial. In Director Present 1-object trials, there was no need to take into account the director’s perspective to identify the correct object (e.g., “Move the turtle left”), as there were no distractors or other referents, and so this resembled a bottom-up, visual pop-out as opposed to a visual search (Buschman & Miller, 2007). The Director Absent condition was logically equivalent, but the directors were replaced by symbolic cues (see Figure 1B).

We previously obtained results on this task in a group of adult participants (Dumontheil, Küster, et al., 2010). Selection of an appropriate action when faced with alternatives (3-object vs. 1-object contrast, collapsed across Director Present and Director Absent conditions) was associated with domain-general bilateral brain activations located primarily in the fronto-parietal cortex, with additional activations in the inferior temporal cortex. Processing of social (Director Present) versus symbolic information (Director Absent) was associated with specific activations in the superior dorsal MPFC and STS. Finally, using perspective taking in this communicative context (Director \times Object interaction), which required participants to think not only

Figure 1. Examples of a 3-object trial in the Director Present (A) and the Director Absent (B) conditions. In both conditions in this example, participants hear the instruction: “Move the large ball up” in either a male or female voice. In both examples, if the voice is female, the object to be moved would be the basketball, because in the Director Present condition (A) the female Director is standing in front of the shelves and can see all the



objects, whereas in the Director Absent condition (B) the two boxes below the “F” (for “female”) indicate that all objects can be moved by the participant. If the voice is male, the object to be moved would be the football, because in the Director Present condition (A) the male Director is standing behind the shelves and therefore cannot see the larger basketball in the occluded slot, whereas in the Director Absent condition (B) the single clear box below the “M” (for “male”) indicates that only objects in open shelves can be moved.

about what the other person sees, but also about his or her intentions, led to further recruitment of superior dorsal MPFC and the left middle temporal gyri, extending into the temporal pole.

The focus of the current study was the difference between the adolescent and adult groups in these three contrasts of interests: (1) 3-object > 1-object; (2) Director Present > Director Absent; and (3) Director \times Object. In line with the adult data, we expected activation in the cognitive control fronto-parietal regions for the first comparison and activation in the social brain network in the latter two comparisons, which contrast the presence of social versus symbolic information and the specific perspective taking requirement. In terms of developmental effects, for the first comparison, as the direction of changes in parietal and frontal cortex activations with age in cognitive control tasks is inconsistent in the literature and may be task dependent, we tested for both developmental increases and decreases in the 3-object vs. 1-object comparison. Regarding the second and third comparisons, the social brain has shown more reliable decreases between adolescence and adulthood in MPFC activations (Blakemore, 2008) and increases in temporal cortex activations (Burnett et al., 2011; Blakemore, 2008) in a variety of social cognition tasks. Our predictions thus aligned with this previous literature: We predicted decreased MPFC activation and increased temporal cortex activation with age in the Director Present versus Director Absent comparison and/or more specifically in the Director Present 3-object condition, which requires on-line use of perspective taking information. Regarding the MPFC, our prediction was focused on the dorsal MPFC on the basis of our previous results in adults as well as the association between this region and mentalizing judgments performed toward others (in this case, the Directors) rather than the self.

METHODS

Participants

Fourteen adult (mean age = 24.9 years, $SD = 3.0$ years, range = 21.3–30.6 years) and 14 adolescent (mean age = 14.0 years, $SD = 1.6$ years, range = 11.6–16.8 years) right-handed female volunteers were included in the analyses (two additional adolescent participants performed poorly on the task due to malfunctioning headphones and were excluded). All participants spoke English fluently and had no history of psychiatric or neurological disorder. Adult participants or the parents of the adolescent participants gave informed consent, and the study was approved by the local ethics committee. General ability was assessed using the two subtests' format (Vocabulary and Matrix Reasoning) of the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999). Estimated IQ normalized for age did not significantly differ between the adolescents (mean IQ = 122,

$SD = 12$, range = 106–140) and adults (mean IQ = 110, $SD = 10$, range = 100–134; $t(26) = 0.735$, $p = .47$).

Design and Stimulus Material

Stimuli consisted of sets of 4×4 shelves with objects located in half of the shelves. Five of the shelves had a gray background (Figure 1). On each trial, participants were given instructions via headphones, by either a male or a female voice, to move one of the eight objects in the shelves to a different slot, either up, down, left, or right (note that this was the participant's left or right). A 2×2 factorial within-subject design was used with the factors Director (Present vs. Absent) and Object (1-object vs. 3-object) varying between blocks.

Director Factor

In the Director Present (DP) condition, the display included two directors, one female and one male. In the Director Absent (DA) condition, there were no directors in the display (Figure 1). Instead, the letters "F" for female and "M" for male were shown beside the shelves. Below each of the letters, there was either one transparent box, which indicated to participants that only objects in open shelves should be moved, or two boxes, one gray and one transparent, which indicated that there was no restriction on the participant's choice and all objects (both in open shelves and occluded shelves) could be moved. For example, in Figure 1B, if participants heard the male voice say, "Move the large ball up," they would need to reason that, because the M is above one clear box, they could only pick objects in clear shelves and thus should ignore the basketball in the gray slot and move the football. These rules had precisely the same consequences as the position of the director in the DP blocks. In DP blocks, the physical position of the director issuing the instruction varied on a trial-by-trial basis; similarly, in DA blocks, the M/F rules changed on a trial-by-trial basis.

Object Factor

Instructions in 1-object blocks (e.g., in Figure 1, "Move the turtle left") referred to a unique target object (there was only one turtle), which was in an open shelf. Instructions in 3-object blocks (e.g., "Move the large ball up") could refer to an object in a closed shelf (with a gray background) or an object in an open shelf, which could both be described with the same instruction (e.g., "large ball"). Which of the possible referents was in fact correct was determined by whether the director giving the instruction (identified as male or female by his or her voice) was at the back or front of the shelves (in DP) or whether the cues indicated that only objects in open shelves could be moved (in DA). This manipulation ensured that in DP 3-object blocks, participants had to consider the director's perspective (which was different from their own perspective on

50% of the trials) to know which was the correct object to move. In DP 1-object blocks, the director's perspective made no difference to the correct interpretation of his or her instructions, and thus, participants could use their own perspective to select the appropriate object on all trials. In the DA condition, perspective taking was not involved.

There were 48 object-shelf configurations, each containing eight objects. Sets of three exemplars of the same object were used for 3-object trials (e.g., three drums). These objects differed in either size (large/small) or position (top/bottom) and were distributed so that the smallest/largest or topmost/bottommost object identified in the instruction was in a closed shelf and the second smallest/largest or topmost/bottommost object and the remaining object were in open shelves. Five additional unique objects were distributed in three gray-backed closed shelves and two open shelves. Those objects in the open shelves could be used for 1-object trials.

To move objects, participants used a trackball mouse, rolling the trackball with their thumb and pressing the left mouse button with the index finger of their right hand. On each trial, participants first moved the mouse cursor from the middle of the screen to the selected object, then clicked on the object, and dragged it to the appropriate slot, before releasing the mouse button. RTs were calculated as the delay between the presentation of the visual stimulus and the pressing of the mouse button. Accuracy was measured on the basis of which object was moved.

On each trial, the visual stimulus and the auditory instruction were presented over a period of 2.2 sec, after which the display remained on the screen for another 3.8 sec. Between trials, a blank screen was shown for 200 msec. The task was programmed with Cogent 2000 and Cogent Graphics (www.vislab.ucl.ac.uk/cogent.php) implemented in Matlab 6.5 (Mathworks, Inc., Sherborn, MA). Standardized instructions were read to participants and included example stimuli in which they had to state which objects should be moved for the different directors and voices. A practice session including one block of each of the four conditions was run outside the scanner to ensure that participants understood the task and could perform it correctly. If a participant did not take into account the director's perspective appropriately, this was highlighted and the task requirements were explained again. Participants also practiced using the trackball mouse ahead of scanning and in the scanner (see Dumontheil, Kuster, et al., 2010).

Participants performed three scanning sessions (two adolescent participants performed two sessions only because of time constraints). Each session consisted of 16 task blocks with four trials in each block. There were four types of experimental block: DA 1-object; DA 3-object; DP 1-object; DA 3-object. Each of the 48 object-shelf configurations was shown once in each block type; thus, there were 12 blocks of four trials for each block type.

Task blocks lasted 24.8 sec and were preceded by an instruction screen presented for 2 sec, which indicated whether the upcoming block was a DP or DA block. The order of the four block types was counterbalanced within and between sessions. A fixation baseline block lasting 20 sec was included after each set of four task blocks.

fMRI Data Acquisition

3-D T₁-weighted fast-field echo structural images and multislice T₂-weighted echo-planar volumes with BOLD contrast (repetition time = 3 sec; echo time = 50 msec; acquisition time = 2.9143 sec) were obtained using a 1.5-T MRI scanner (Siemens TIM Avanto, Erlangen, Germany). Functional imaging data were acquired in two or three scanning sessions lasting approximately 8 min 40 sec each in which 174 volumes were obtained. The first two volumes of each session were discarded to allow for T₁ equilibrium effects. Each functional brain volume was composed of 35 axial slices with an in-plane resolution of 3 × 3 × 3 mm, positioned to cover the whole brain. A T₁-weighted anatomical image lasting 5 min 30 sec was acquired after the first two functional sessions for each participant.

Data Analysis

Behavioral Data

RTs and accuracy in all four conditions were recorded and analyzed using a 2 (Age Group: Adolescents vs. Adults) × 2 (Director: DA vs. DP) × 2 (Object: 1-object vs. 3-object) mixed model repeated-measures ANOVA to investigate the effects of each task factor, the interaction between task factors and their interaction with age.

fMRI Data

fMRI image preprocessing and analysis were carried out using SPM8 (Wellcome Department of Imaging Neuroscience, London, UK), implemented in MATLAB 7.8 (Mathworks, Inc., Sherborn, MA). To correct for movement effects, images were realigned with a fourth-degree B-spline interpolation. These realigned images were corrected for differences in acquisition times and were then normalized to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain. The resulting 3 × 3 × 3 mm images were finally spatially smoothed with an 8-mm FWHM Gaussian kernel. Analyses of the movement parameters showed that translation within each session was <3 mm in all participants. Mean movement per session was calculated for translations and rotations in each direction for each subject. Independent *t* tests were used to compare the means of these values over the sessions between the two age groups. There was no significant difference for translations [all $t(26) < .43, p > .67$] nor for rotations [all $t(26) < .28, p > .78$].

For each participant, the scanning sessions were treated as separate time series; statistical parametric maps were created and estimated using a general linear model for each time series (Friston et al., 1995). Included in the model were six boxcar regressors, modeling the instruction, fixation and four types of task blocks, plus one event-related regressor representing error trials. All regressors were convolved with a canonical hemodynamic response function and, together with regressors representing residual movement-related artifacts and the mean over scans, comprised the full model for each session. The data and model were high-pass filtered to a cut-off of 1/128 Hz. Parameter estimates calculated from the least mean squares fit of the model to the data were used in four pairwise contrasts comparing each block type with the fixation baseline. These contrasts were entered into a Condition \times Age Group \times Participant flexible factorial design second-level analysis. The factor participant was included to model the repeated aspect of the data. Main effects of Object (3-object > 1-object) and Director (DP > DA and DA > DP) and the interaction between the two factors and with age group were determined using the t statistic on a voxel-by-voxel basis. Statistical contrasts were used to create SPM{Z} maps thresholded at $p < .001$ at the voxel level and at family-wise error (FWE)-corrected $p < .05$ at the cluster level (corresponding to a minimum cluster size of 82 voxels determined with SPM8). Activations that survived whole-brain FWE correction at $p < .05$ are indicated. Analyses performed with age as a continuous regressor did not highlight any regions not observed with the age group analyses and are thus not reported. All coordinates are given in MNI space. ROI analyses based on the main effect of DP > DA were further performed to test for orthogonal interaction effects between the Director, Object, and Age Group factors in the brain regions identified as responding to the social stimuli. Additional analyses explored possible continuous effects of age and differences between the seven youngest and seven oldest adolescent

participants and the adults. Note that these analyses are limited by the age range gap between 17 and 21 and underpowered by the small N of the adolescent subgroups. Statistical threshold for the ROI analyses performed in SPSS was $p < .05$ (two-tailed).

RESULTS

Behavioral Results

Accuracy was calculated for each of the four conditions in each session. Four sessions (from three participants) were discarded from further analyses because of poor performance in one of the conditions (accuracy < 50%). Included in the analyses were thus 14 adults (13 with three sessions, 1 with two sessions) and 14 adolescents (10 with three sessions, 3 with two sessions, 1 with one session). Accuracy and median RTs in correct trials were analyzed using a 2 (Age Group: Adolescent, Adult) \times 2 (Director: DP vs. DA) \times 2 (Object: 1-object vs. 3-object) mixed model repeated-measures ANOVA.

Accuracy was higher in the DP than in the DA condition [main effect of Director, $F(1, 26) = 6.29, p = .019$] and higher in 1-object than 3-object blocks [main effect of Object, $F(1, 26) = 38.29, p < .001$; Figure 2A]. There was no main effect of age group ($p > .6$) and no interaction between age group and the task factors (all interaction p values > .22). A similar pattern of performance was observed in terms of RTs. Participants were faster in the DP than DA condition, $F(1, 26) = 48.36, p < .001$, and in 1-object than 3-object blocks, $F(1, 26) = 465.16, p < .001$, and there was no main effect of age and no interaction with age group (all $ps > .24$). However, there was a significant interaction between Director and Object, $F(1, 26) = 15.69, p < .001$, reflecting a greater effect of Object in the DA condition (Figure 2B). Thus, effects of Director and Object were observed on both measures

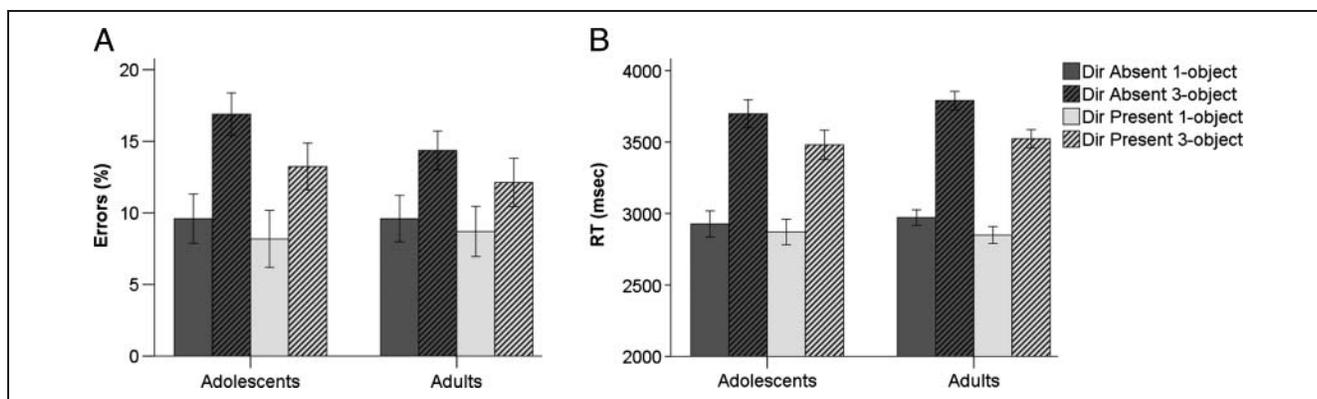


Figure 2. Behavioral performance. (A) Percentage errors (mean \pm SE) in each of the four conditions, plotted separately for the two age groups. There was no main effect of age group and no interaction between age group and condition. However, overall, participants made more errors in 3-object than 1-object blocks and more errors in the Director Absent than Director Present condition. (B) Median RT (mean \pm SE) in each of the four task conditions, plotted separately for the two age groups. A similar pattern of effects of the Object and Director factors was observed for RTs as for accuracy. In addition, the interaction between the Object and Director factors was significant, with a larger RT difference between 3-object and 1-object trials in Director Absent (mean = 795 msec) than in Director Present (mean = 642 msec).

Table 1. Coordinates and Z Values for Regions of Significant Differences in BOLD Signal in the Main Effect Contrast of Object [3-Object > 1-Object] and the Interaction between Object and Age Group [(Adults 3-Object > 1-Object) > (Adolescents 3-Object > 1-Objects)] ($p < .001$ Uncorrected at the Voxel-level, $p < .05$ FWE Corrected at the Cluster Level)

	<i>L/R</i>	<i>Brodmann's Area</i>	<i>MNI (x y z)</i>	<i>Z Score</i>	<i>p(FWE)*</i>	<i>Cluster Size</i>
<i>Main Effect of Object: 3-Object > 1-Object</i>						
Superior parietal lobule	R	7	27 -64 52	>8	<.001	14181
IPS	L	40	-39 -49 46	>8	<.001	
MTG/occipital gyrus	R	39/19	42 -79 22	>8	<.001	
SFS	R	6	30 -4 64	>8	<.001	
Precuneus	R	7	6 -64 49	>8	<.001	
SFS	L	6	-21 -4 52	>8	<.001	
IFG	R	44	48 8 34	>8	<.001	
MFG	R	9	45 26 31	>8	<.001	
Supramarginal gyrus	R	40	39 -40 40	>8	<.001	
Precentral gyrus	L	6	-42 2 37	>8	<.001	
ITS	R	37	48 -55 -14	7.61	<.001	
Occipital gyrus	L	19	-39 -73 -11	6.75	<.001	
MFG	L	9	-45 23 40	6.32	<.001	
MFG	L	10/46	-42 47 7	6.22	<.001	
Medial SFG	R	6	6 14 49	6.20	<.001	
Thalamus	L		-12 -16 10	4.93	.010	117
<i>Age Group × Object Interaction: Adults > Adolescents (3-Object > 1-Object)</i>						
Precentral gyrus	L	6	-45 5 31	4.96	.009	368
Inferior frontal gyrus	L	45	-42 23 22	4.60		
Insula	L		-39 17 7	4.12		
IPS/supramarginal gyrus	L	40	-45 -49 43	4.27	.018	110

IFG = inferior frontal gyrus; IPS = intraparietal sulcus; ITS = inferior temporal sulcus; MFG = middle frontal gyrus; MTG = middle temporal gyrus; SFG = superior frontal gyrus; SFS = superior frontal sulcus; L/R: left/right.

*Voxel-wise whole-brain FWE-corrected p -value, where $p < .05$.

of performance, but the adolescents' and adults' performance did not differ.

fMRI Results

The four first-level contrasts comparing each block type [Director (2) × Object (2)] to fixation were entered in a flexible factorial second-level analysis, including age group and participant as factors.

Object Factor

A broad bilateral network of fronto-parietal, occipital, and inferior temporal regions showed increased BOLD signal in 3-object compared with 1-object blocks (Table 1 and

Figure 3A), that is, when the participants had to identify a specific object to move among three exemplars of the same object type (e.g., one of several balls on Figure 1) as opposed to when there was only one exemplar of the object (e.g., the turtle on Figure 1). Greatest increases in BOLD signal were observed bilaterally in superior and inferior parietal lobules, superior frontal sulci, and precuneus. Other regions included the medial superior frontal gyrus and anterior parts of PFC in the middle frontal gyri bilaterally.

Object and Age Group factors significantly interacted in fronto-parietal regions in the left hemisphere. Adults showed increased BOLD signal in the 3-object vs. 1-object blocks, compared with adolescents, in the intraparietal sulcus and in a cluster extending from the precentral gyrus to the inferior frontal gyrus and insula (Table 1 and

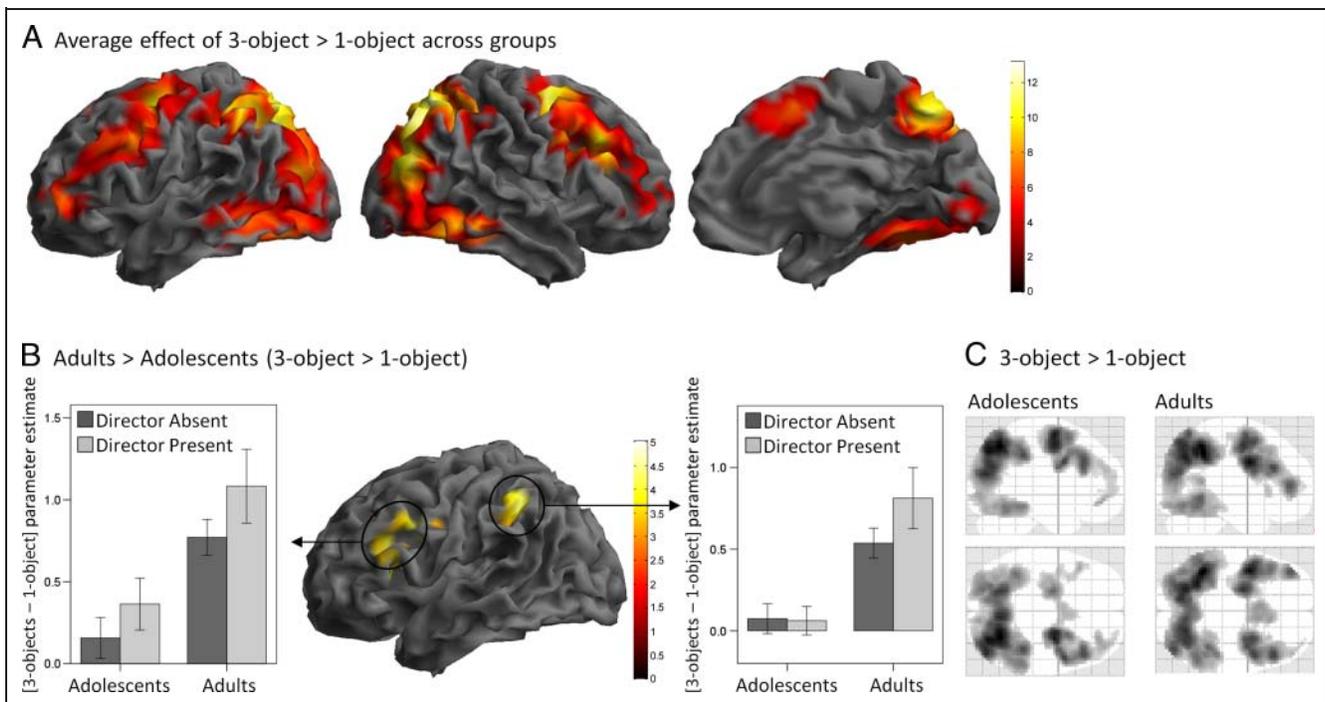


Figure 3. Effect of the Object factor and interaction between Object and Age Group. (A) Main effect of the Object factor. Regions showing increased BOLD signal in 3-object compared with 1-object blocks across age groups are rendered on the SPM8 surface mesh template. From left to right: lateral view of the left hemisphere, lateral and medial views of the right hemisphere. (B) Object \times Age Group interaction. Regions showing increased BOLD signal in 3-object compared with 1-object trials in the adults compared with the adolescents are rendered on the SPM8 surface mesh template (lateral view of the left hemisphere). Parameter estimates were extracted and plotted for the two significant clusters, in the left intraparietal sulcus (mean of 110 voxels) and the left lateral PFC (mean of 368 voxels). (C) On the right, glass brain representations show the regions of increased BOLD signal in the 3-object compared with 1-object blocks in each age group separately. Contrasts were thresholded at $p < .001$ uncorrected at the voxel level, $p < .05$ FWE corrected at the cluster level.

Figure 3B). This significant interaction between Object and Age Group reflected more bilateral activations in frontal and parietal regions in adults than adolescents (Figure 3C). Note that these two clusters remained significant when mean RT and accuracy for each condition and participant were entered as covariates in the second-level analyses [left frontal cluster: $Z = 4.84$, $p(\text{FWE}) < .001$, 326 voxels; left parietal cluster: $Z = 4.27$, $p(\text{FWE}) = .029$, 96 voxels].

Both younger and older adolescent subgroups showed weaker 3-object than 1-object fronto-parietal activation than adults ($ps < .05$) and did not differ from each other (parietal region: $p > .5$; frontal region: $p = .066$, trend for greater activation in the younger adolescents). The activation in 3-object vs. 1-object trials also significantly increased with age entered as a continuous variable ($ps < .01$), although this effect was less significant than the Age Group effect.

Director Factor

When comparing the Director Present condition to the Director Absent condition, that is, when the cues were social stimuli rather than symbols, increased BOLD signal was observed in bilateral superior and middle temporal cortex regions along the STS and extending into the ante-

rior temporal cortex, as well as in the right inferior frontal gyrus, dorsal MPFC, precuneus, and occipital gyrus (Table 2 and Figure 4A). The reverse contrast, that is, when the cues were not social but symbolic and rule-based, revealed increased BOLD signal in the left parietal cortex only (Table 2 and Figure 4A). There was no significant interaction between Director and Age Group factors.

Director \times Object Interaction

Whole-brain analyses at the cluster FWE-corrected threshold $p < .05$ showed no brain regions with significant Director \times Object or Director \times Object \times Age Group interactions. An ROI approach (which is potentially less robust because it is biased toward particular clusters) was thus used as follows: mean parameter estimates were calculated for all clusters of the DP > DA contrast and analyzed in SPSS using a mixed model repeated-measures ANOVA. The ROI clusters were in the left temporal cortex, right temporal cortex, occipital gyrus, dorsal MPFC, precuneus, and right inferior frontal gyrus (see Table 2 and Figure 4A).

Director \times Object and Director \times Object \times Age Group interactions were tested using mixed repeated-measures ANOVAs on the mean parameter estimates in these ROIs. The aim was to identify regions that showed increased BOLD signal when participants had to take into account

the Directors' perspective to perform the task correctly. A significant Director \times Object interaction was observed in the left temporal cortex cluster, $F(1, 26) = 6.12, p = .020$, and in the dorsal MPFC cluster, $F(1, 26) = 4.87, p = .036$. In both cases, the difference in BOLD signal between DP and DA was greater in 3-object than 1-object trials. In addition, the Director \times Object \times Age Group interaction was significant in the dorsal MPFC cluster, $F(1, 26) = 4.76, p = .038$. This

three-way interaction reflected the fact that the difference between DP and DA was greater in 3-object than 1-object trials in adults ($p = .014$) but not in adolescents ($p > .9$; Figure 4B). Adolescents thus showed greater BOLD signal in DP than DA in both 1-object and 3-object trials, whereas adults showed a greater DP than DA activation in 3-object trials specifically, that is, when the perspective of the directors needed to be taken into account.

Table 2. Coordinates and Z Values for Regions of Significant Differences in BOLD Signal in the Main Effect Contrasts of the Director Factor ($p < .001$ Uncorrected at the Voxel Level, $p < .05$ FWE Corrected at the Cluster Level)

	L/R	Brodmann's Area	MNI (x y z)	Z Score	$p(\text{FWE})^*$	Cluster Size
<i>Main Effect of Director: Director Present > Director Absent</i>						
MTG/STS	L	39	-45 -73 13	7.53	<.001	1537
STG/STS	L	22	-54 -46 13	5.53	.001	
MTG	L	21	-48 2 -26	4.91	.011	
Fusiform gyrus	L	37	-39 -40 -17	4.81	.017	
MTG/STS	L	21	-54 -10 -14	4.79	.018	
Hippocampus	L		-33 -10 -20	4.36		
SOG/Cuneus	L	17/18	-12 -94 4	7.15	<.001	253
MTG/STS	R	22/39	57 -58 13	6.34	<.001	952
STG/STS	R	22	51 -46 16	5.13	.004	
MTG	R	21	51 5 -20	4.33		
STG/STS	R	21	48 -31 1	3.9		
MTG	R	21	51 -16 -8	3.87		
Precuneus	L	7	-6 -52 43	5.41	.001	325
Precuneus	L	7	-12 -52 31	4.59	.042	
Cingulate gyrus	R	31	6 -55 28	4.3		
Medial SFG	L	8	-12 47 46	4.98	.008	533
SFG	L	8	-18 38 55	4.84	.015	
Medial SFG	L	10	-6 56 25	4.06		
Medial SFG	L	10	-9 50 16	3.97		
Medial SFG	R	9	6 53 37	3.94		
SFG	L	8	-21 26 49	3.91		
Cingulate gyrus	L	32	-12 47 4	3.45		
IFG	R	45	57 29 4	4.59	.042	85
<i>Main Effect of Director: Director Absent > Director Present</i>						
Middle occipital gyrus	L	19	-24 -67 37	5.19	<.001	362
Intraparietal sulcus	L	40	-30 -55 46	4.80		
Supramarginal gyrus	L	7	-42 -55 61	3.94		

IFG = inferior frontal gyrus; MTG = middle temporal gyrus; SFG = superior frontal gyrus; SOG = superior occipital gyrus; STG = superior temporal gyrus; STS = superior temporal sulcus; L/R = left/right.

*Voxel-wise whole-brain FWE-corrected p -value, where $p < .05$.

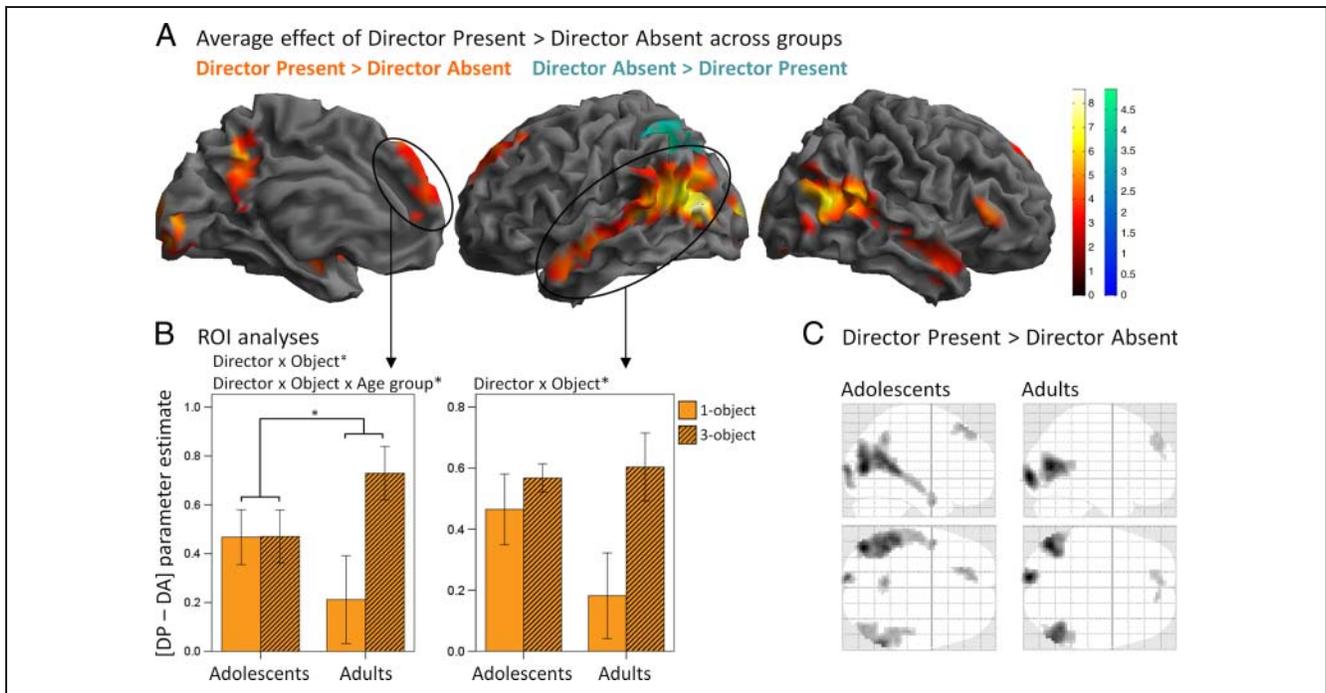


Figure 4. Effect of the Director factor and interaction with Object and Age Group. (A) Main effect of the Director factor across age groups. Regions showing increased BOLD signal in the Director Present compared with Director Absent blocks (in yellow–red color scale) or in the reverse Director Absent compared with Director Present blocks (in green–blue color scale) are rendered on the SPM8 surface mesh template. From left to right: medial and lateral view of the left hemisphere, lateral view of the right hemisphere. (B) ROI analyses testing for interactions between Director and Object and between Director, Object, and Age Group. Mean parameter estimates in two clusters of the Director Present > Director Absent contrast across age groups showed a significant interaction between Director and Object factors, with greatest activation in the DP 3-object condition (left temporal cluster, extending along the middle temporal gyrus and STS, mean of 1537 voxels; superior dorsal MPFC cluster, mean of 533 voxels). The superior dorsal MPFC cluster showed a further significant three-way interaction between Director, Object, and Age Group, with a significant increase in [DP – DA] in 3-object vs. 1-object blocks in the adults only. (C) Director Present vs. Director Absent contrast in each age group. Contrasts were thresholded at $p < .001$ uncorrected at the voxel level, $p < .05$ FWE corrected at the cluster level.

Although the Object \times Age Group interactions of DP vs. DA did not reach significance when comparing the younger and older adolescent subgroups to the adults ($p = .071$ and $p = .152$, respectively), the same pattern of no difference in DP vs. DA activation between 3-object and 1-object trials ($ps > .7$) was observed in both adolescent groups. Similarly, the interaction between Object and Age Group as a continuous variable for DP vs. DA activation ($p = .2$) did not reach significance, suggesting the developmental effect was best accounted for by group (adolescents vs. adults).

DISCUSSION

This study investigated the development of the neural substrates of action selection when the information guiding the choice is symbolic or social in nature, which enabled us to investigate domain-general processes (common to the symbolic and social conditions) and domain-specific processes (specific to the social or symbolic conditions). The paradigm we used required participants to take the perspective of another person in an implicit manner and respond appropriately in a communicative context. First, we showed that the fronto-parietal and temporal brain network showing increased BOLD signal when participants

had to identify a target among distractors showed greater BOLD signal in adults than adolescents in the left lateral PFC and parietal cortex (Figure 3). Second, the processing of social versus symbolic stimuli led to social brain network activations in the superior dorsal MPFC, precuneus, and large temporal clusters; the reverse contrast showed activation in the left parietal cortex only, in a region sensitive to the Object factor (Figure 4). Although no whole-brain interaction effects were observed, ROI analyses were performed on those clusters showing greater activations in Director Present than Director Absent trials to investigate specific BOLD signal increases associated with the use of social versus symbolic cues to guide the selection of the appropriate target among the distractor objects. The left temporal cluster and dorsal MPFC regions showed an interaction between Director and Object, with increased BOLD signal in Director Present 3-object trials, when the perspective of the director needed to be taken into account. The dorsal MPFC region showed a further significant three-way interaction, between Director, Object and Age Group, showing that the adults, but not the adolescents, exhibited specifically greater Director Present than Director Absent activation in 3-object trials. Adolescents showed greater BOLD signal in the superior dorsal MPFC in Director

Present than Director Absent both in 1-object and 3-object trials (Figure 4).

Development of the Integration of Information to Guide Action Selection

The comparison between trials requiring the identification and selection of one of three objects compared with a single target object highlights brain regions recruited in top-down control of attention and goal-directed action. Participants needed to remember the instruction and integrate it with the social or symbolic rule-based cues to identify which of the three exemplar of the target object (e.g., ball) is the correct one to move. All participants were slower and less accurate in 3-object than 1-object trials, but the age groups did not differ (Figure 2). Over the whole group of participants, a large bilateral network of brain regions showed greater BOLD signal in 3-object compared with 1-object blocks of trials (Figure 3A). Frontal and parietal cortices have been proposed to be the source of spatial attentional modulation of the ventral visual system during object recognition or discrimination (Beck & Kastner, 2009; Tong, 2003; Corbetta, 1998; Corbetta & Shulman, 1998). This network has also been shown to drive nonspatial, feature-based (e.g., color) selective attention (Giesbrecht, Woldorff, Song, & Mangun, 2003). The network observed in the current study includes the fronto-parietal cortex clusters (see Table 1) identified as supporting top-down or endogenous control of selective attention in a spatial cueing paradigm (Hahn et al., 2006) and also those observed in a spatial and feature cueing paradigm (Giesbrecht et al., 2003) and in a visual search paradigm (Booth et al., 2003). Differences in the location of occipital activations and in the spread of activations between these paradigms and the current study may relate to the cueing in this study being partly based on auditory verbal stimuli and/or to the greater complexity of the visual stimuli in this study.

There is little previous research regarding neural changes associated with the development of selective attention. Booth et al. (2003) report greater activations in the left thalamus and the right anterior cingulate in children (aged 9–11 years old) compared with adults (aged 20–30 years) when contrasting a nine-stimuli array visual conjunction search to a simple stimulus detection response; no brain region showed greater activation in adults than in children. In the present study, the target stimuli varied on a trial-by-trial basis, thus BOLD signal changes during the task reflect the encoding and integration of the auditory and visual target information, in addition to the simpler visual detection of the appropriate target shape (e.g., a ball). The developmental results obtained in the current study revealed increased BOLD signal in adults compared with adolescents in the left precentral gyrus extending into the inferior frontal gyrus and in the left intraparietal sulcus/supramarginal gyrus when comparing 3-object with 1-object trials (Figure 3B). The literature on the development of

the neural substrates of attention and cognitive control has not shown a consistent direction of changes in BOLD signal with age (Luna et al., 2010). However, lateral PFC and parietal cortex are key regions that consistently show developmental changes. Overall, the pattern of results in the literature suggests that, although core regions of the circuitry underlying cognitive control are on-line early in development, the network of brain regions underlying, for example, working memory is still developing during adolescence (Crone & Ridderinkhof, 2010; Luna et al., 2010). The current 3-object versus 1-object comparison contains a combination of attention (visual search), working memory (remembering the rule, instruction and already attended aspects of the stimuli), and inhibition demands (inhibiting attention toward the distractor stimuli and its associated response). In this context, the results show that adolescent development is associated with increasingly bilateral frontal and parietal activations.

In summary, this study shows fronto-parietal and temporal cortex activations when participants are required to integrate complex visual and auditory information to search and select one of two possible actions versus when the action to perform is more simply identified. Despite similar performance, adolescents show hypoactivation of the left frontal and parietal cortex.

Processing of Social versus Symbolic Information

The instructions were fully matched between the Director Present and Director Absent conditions. However, the visual stimuli differed, with two characters standing in front or at the back of the set of shelves in the Director Present condition, versus the letters F and M and gray or transparent boxes in the Director Absent condition. Main effects of Director were observed for both accuracy and RTs, with better performance in the Director Present condition. Previous research using a behavioral variant of the Director task showed both young and adult participants were much more error prone in the Director Present condition (Apperly et al., 2010; Dumontheil, Apperly, et al., 2010). However, these studies investigated participants' natural tendency to take into account the director's perspective. In this study, participants went through a training session where their performance was corrected if they did not take into account the directors' perspectives. This aspect of the task was stressed as important, and accordingly, we obtained high accuracy rates. The performance benefit associated with the social versus the symbolic stimuli is in line with previous studies showing that participants perform faster (den Ouden, Frith, Frith, & Blakemore, 2005) and more accurately (Baron-Cohen et al., 1986) on social compared with nonsocial tasks.

fMRI results showed that the presence of the symbolic stimuli was associated with greater activation in the left parietal cortex only, which overlapped with the network of regions more active in the 3-object than 1-object condition (Figure 4A). Conversely, the presence of the social

stimuli was associated with greater activation in a large bilateral network of temporal, precuneus, and dorsal MPFC regions that mostly did not overlap with those regions more activated in the 3-object than 1-object contrast, except in the posterior parts of the middle temporal gyrus bilaterally, the precuneus, and part of the left superior occipital gyrus (Figure 4A). Thus, the presence of social stimuli led to increased BOLD signal in a number of regions that form the social brain network, from face and eye gaze-sensitive brain regions along the STS (Haxby, Hoffman, & Gobbini, 2000), body-sensitive regions in the extrastriate body area (Taylor, Wiggett, & Downing, 2007), to mentalizing regions in the posterior STS and the MPFC (Frith & Frith, 2003; Gallagher & Frith, 2003). More specifically, the STS activation observed in this Director Present versus Director Absent contrast extends into a pSTS region previously observed to show increased BOLD when participants planned or recognized each other's communicative intentions (Noordzij et al., 2010). The MPFC activation was dorsal and aligned with the activations observed in tasks requiring mentalizing or trait judgments made on others rather than judgment made on the self (Van Overwalle, 2009; Mitchell et al., 2006). In addition, although the MPFC activation observed in the current study is located in quite a superior dorsal part of the MPFC, recent meta-analyses suggest that mentalizing activations extend over a wide range of coordinates in the MPFC (Van Overwalle, 2009, 2011) and that non-story-based theory of mind studies tend to show more superior activations than story-based theory of mind studies (Mar, 2011). The Director Present condition also likely led participants to associate the male or female voice heard with the male or female director character presented visually. Activations along the STS have been reported in a study of the encoding of speaker identity in the cortical surface (Formisano, De Martino, Bonte, & Goebel, 2008), and the STS has been shown to represent the integration of auditory-visual integration of faces and voices (Chandrasekaran & Ghazanfar, 2009).

It is noteworthy that the current Director Present versus Director Absent contrast was collapsed across a condition requiring participants to take into account the director's perspective (3-object) and a condition where the director's perspective was not necessary to identify the target object (1-object). Thus, here, the mere presence of the directors and possibly the integration of the auditory instruction and the director's visual representation (Chandrasekaran & Ghazanfar, 2009; Formisano et al., 2008) were sufficient to elicit activations in the mentalizing network. This finding is consistent with the suggestion that MPFC plays a broad role in general social cognition (Saxe & Powell, 2006; see also Saxe, Whitfield-Gabrieli, Scholz, & Pelphrey, 2009). An alternative account is that, although mentalizing was not necessary in the 1-object condition, participants nonetheless computed the director's perspective. We did not make a distinction between 1-object and 3-object blocks during the training phase or during scanning; thus, participants may

have computed the director's perspective on all trials rather than deciding whether it was necessary to do so on a block-by-block or trial-by-trial basis. In line with this interpretation, previous research provides evidence that mentalizing can happen even when it is unnecessary (e.g., Back & Apperly, 2010; Kovacs, Teglas, & Endress, 2010) and even when it actively impedes performance on the main task (e.g., Qureshi, Apperly, & Samson, 2010; Samson, Apperly, Braithwaite, Andrews, & Bodley Scott, 2010).

Our second prediction was that the Director Present vs. Director Absent comparison may show age-related decreases in activation in the dorsal MPFC and increases in the temporal cortex, associated with the processing of social information. No significant Age Group \times Director interaction was observed, suggesting that the age groups in fact did not differ in their average social brain response to the Director Present stimuli. To summarize, in this study we observed both domain-general activations in cognitive control regions (3-object vs. 1-object contrast) and domain-specific activations associated with the processing of social cues (Director Present vs. Director Absent contrast).

The Use of Perspective Information to Guide Action Selection

The reliance on social cues was associated with faster RTs than the use of symbolic cues in 3-object trials (compared with responses in 1-object trials; Figure 2B). Whole-brain analyses did not reveal regions exhibiting an interaction between Director and Object factors, and Director, Object, and Age Groups. However, ROI analyses of the clusters obtained in the Director Present vs. Director Absent contrast showed that the left temporal and superior dorsal MPFC clusters exhibited increased activation in the DP 3-object condition (Figure 4B). In the superior dorsal MPFC, this Director \times Object interaction was further modulated by Age Group, reflecting the fact that the increase in BOLD signal in DP 3-object trials was observed in the adults only (Figure 4B). Our third prediction was that age effects on the social brain activation, in particular, in the MPFC and temporal cortex, if not observed in the Director Present versus Director Absent contrast, might have been more specific to the Director Present 3-object condition, which requires the on-line use of perspective taking information. Our results do show significant age effects in dorsal MPFC (although the pattern in the temporal cortex is qualitatively similar, there was no significant interaction with Age Group); however, the pattern of changes in activation with age is more complex than that predicted from the literature and discussed below. Note that a limitation of this study is that these findings obtained using ROI analyses are consequently weaker than the whole-brain findings described in the previous sections.

Although small, the three-way interaction with age observed in the current study provides interesting new information regarding the development of the social brain

during adolescence. Previous studies have consistently reported greater MPFC activations in adolescents than adults in a variety of social cognition tasks (see Blakemore, 2008, for a review of the earlier studies; Gunther Moor et al., 2012; Sebastian et al., 2012; Pfeifer et al., 2009; Burnett, Bird, Moll, Frith, & Blakemore, 2008). The tasks used typically required participants to make an explicit judgment regarding the mental states of a character in a scenario presented in animations (Moriguchi, Ohnishi, Mori, Matsuda, & Komaki, 2007), drawings (Sebastian et al., 2012; Wang, Lee, Sigman, & Dapretto, 2006), or text (Burnett et al., 2008; Blakemore, den Ouden, Choudhury, & Frith, 2007). Two studies required participants to judge how much a phrase (e.g., “I am popular”) described themselves (Pfeifer et al., 2009; Pfeifer, Lieberman, & Dapretto, 2007), and one study involved participants judging a person’s emotion from photos of their eyes (Gunther Moor et al., 2012). Thus, participants were asked to reflect on their own or someone’s thoughts or emotions in an explicit and somewhat detached manner, and the results showed that in such situations there are greater BOLD signal increases in adolescents than adults in the MPFC. In this study, participants were required to use social cues regarding the perspective and knowledge of another person in an on-line manner and in a communicative context and then to perform the appropriate action. Interestingly, our results show that the adolescents did not recruit dorsal MPFC specifically in the perspective taking condition (Director Present 3-object) but more generally whenever the stimuli had a social aspect, that is, in the comparison of Director Present versus Director Absent. Adults, however, showed greater dorsal MPFC activations that were specific to the Director Present 3-object trials, that is, when information about the director’s perspective had to be taken into account to respond appropriately.

These results cast some light on the possible interpretation of previous findings of greater MPFC activations during mentalizing in adolescents. In previous studies, it is not clear whether this greater MPFC activation is due to adolescents “overmentalizing” in response to the same stimuli, or having to put in more work in terms of neural resources to achieve the same mentalizing computations or to lower signal-to-noise ratio associated with increased prefrontal gray matter volumes in adolescence compared with adulthood (see Blakemore, 2008). Recent work using other tasks suggests that decreases in brain activation during adolescence do not necessarily reflect concomitant gray matter volumes decreases (Dumontheil, Hassan, Gilbert, & Blakemore, 2010; Dumontheil, Houlton, Christoff, & Blakemore, 2010). The current study provides no evidence that adolescents use more neural effort to achieve the same mentalizing performance: In the absence of differences in performance, adolescents did not show greater activations than adults in Director Present 3-object trials, which require participants to take the director’s perspective into account. Instead, adolescents appeared to show less

specific mentalizing MPFC activations than adults, with MPFC activations observed at a similar level in Director Present 1-object and 3-object trials. These findings are thus more consistent with the overmentalizing interpretation of the greater MPFC activations observed during adolescence in previous studies. The pattern of results observed in the dorsal MPFC in the current study is similar to the finding of a lack of specificity of right TPJ activation in early childhood in a verbal story-based task (Saxe et al., 2009). Among children aged 6–11 years old, the right TPJ was similarly recruited when the younger children listened to sections of a story describing a character’s thoughts (Mental condition) or appearance and social relationships (People), whereas older children showed right TPJ activation only for the Mental condition (Saxe et al., 2009), thus showing increased right TPJ specificity for theory of mind with age.

To summarize, the current study showed that adolescents exhibited dorsal MPFC activation in both social conditions and did not show the specific increased dorsal MPFC activation observed in adults when the trial required the participant to take into account the director’s perspective to choose the appropriate response.

Ecological Validity of the Task

The communicative nature of the task employed here is more ecologically valid than the previous theory of mind tasks employed in neuroimaging experiments. By using this task, we are addressing recent concerns that story-based theory of mind tasks might add processing demands that are not directly linked to the computation of mental states (Apperly, Samson, Chiavarino, & Humphreys, 2004). Another advantage of our paradigm is that it contributes to the disentanglement of different theory of mind subprocesses: It is seemingly contradictory that infants know what another person can or cannot see (Moll & Tomasello, 2006; Flavell, Abrahams Everett, Croft, & Flavell, 1981) and that adults calculate other people’s perspective automatically (Samson et al., 2010), but that there is a protracted development of performance on our perspective taking task and that even adults have a high error rate. This study adds to the growing body of work that distinguishes between processes that might be relatively specific to theory of mind, perhaps corresponding to social brain network activations, and processes that are domain-general but equally necessary for actually using theory of mind information to select an appropriate action or verbal response, perhaps corresponding to cognitive control network activations (e.g., Samson, Apperly, Kathirgamanathan, & Humphreys, 2005; Saxe et al., 2004, 2006; see Apperly, 2011, for discussion). Here, we have shown that both domain-general and domain-specific activations showed developmental changes. Adolescents showed a combination of weaker lateral PFC activations that were not specific to the social condition and social brain activations, in particular, in the MPFC, that showed less specificity to perspective

taking requirements compared with adults. The hypoactivation of cognitive control regions in the adolescents may be behind the greater egocentric bias observed in a similar paradigm during adolescence (Dumontheil, Apperly, et al., 2010). Future studies with greater number of adolescent participants could investigate in more details the observed effects and test their association with pubertal development as opposed to chronological age only (Blakemore, Burnett, & Dahl, 2010), as well as the connectivity between the cognitive control and social brain networks.

Conclusion

The aim of this study was to investigate the development of the neural substrates associated with the selection of action among distractors and with the use of social cues to guide action selection. We used a novel paradigm that requires participants to use either symbolic rules or perspective information of other individuals to select an appropriate action in a communicative context. Having previously shown that the on-line use of perspective information led to the recruitment of superior dorsal MPFC, left STS, and anterior temporal cortex regions in adults, we showed here that adolescents exhibited hypoactivation of domain-general cognitive control regions in the parietal cortex and PFC and hyperactivation of parts of the social brain network, with dorsal MPFC activation observed whether or not the social cues were necessary to perform the action appropriately. These results provide further evidence of the prolonged development of neural substrates of social cognition. They suggest that the pattern of increased MPFC activations in adolescence associated with explicit mentalizing judgments (Burnett & Blakemore, 2009) is not found when mentalizing has to be used on-line by taking another's perspective in an active communicative context. Instead, MPFC showed increased activations in adolescence in both the 1- and 3-object conditions, whereas adults engaged MPFC more for 3-object condition. This pattern may reflect overmentalizing in adolescence in conditions where mentalizing is not needed (1-object condition).

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Reprint requests should be sent to Dr. Iroise Dumontheil, University College London Institute of Cognitive Neuroscience, 17 Queen Square, London, WC1N 3AR, UK, or via e-mail: i.dumontheil@ucl.ac.uk.

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