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Deciphering human motion to discriminate social interactions: a developmental neuroimaging study

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Abstract

Non-verbal communication plays a major role in social interaction understanding. Using functional magnetic resonance imaging, we explored the development of the neural networks involved in social interaction recognition based on human motion in children (8–11), adolescents (13–17), and adults (20–41). Participants watched point-light videos depicting two actors interacting or moving independently and were asked whether these agents were interacting or not. All groups successfully performed the discrimination task, but children had a lower performance and longer response times than the older groups. In all three groups, the posterior parts of the superior temporal sulci and middle temporal gyri, the inferior frontal gyri and the anterior temporal lobes showed greater activation when observing social interactions. In addition, adolescents and adults recruited the caudate nucleus and some frontal regions that are part of the mirror system. Adults showed greater activations in parietal and frontal regions (part of them belonging to the social brain) than adolescents. An increased number of regions that are part of the mirror system network or the social brain, as well as the caudate nucleus, were recruited with age. In conclusion, a shared set of brain regions enabling the discrimination of social interactions from neutral movements through human motion is already present in 8-year-old children. Developmental processes such as refinements in the social brain and mirror system would help grasping subtle cues in non-verbal aspects of social interactions.

Key words: social brain; fMRI; child; adolescent; point-light

Introduction

From an early age, we use and interpret body language to communicate with other people. The ability to understand others' intentions and actions on the basis of movement analysis is crucial since it allows us to detect important cues in our environment and determines our behavior. Human motion recognition is a key factor in social cognition and provides information about potential social interactions (SIs), which are dynamic sequences of social actions between individuals. Across lifespan, human motion perception and SI recognition may change as general social

cognitive abilities evolve and neural maturation occurs. Despite many studies about body motion recognition, little is known about the neural basis of SI recognition based on human motion information only (Centelles *et al.*, 2011, 2013).

In the 1970s, the psychologist Johansson (1973) developed a technique to explore body motion perception with minimized shape aspects. He used point-lights fixed on the actors' main joints to record scenes on a dark background. His study revealed that information carried by a pattern of moving point-lights was sufficient to recognize human walking, running, or dancing. Human body perception would be already developed in newborns (Filippetti *et al.*, 2013). Biological motion represented by point-lights is sufficient for the recognition of human and non-human forms by 3-year-old children (Pavlova *et al.*, 2001). In addition, a study by Centelles *et al.* (2013) showed that 4-year-old children were already able to discriminate SIs from neutral movements (NMs) using body motion information only. Four-year-old children scored below the adults in this SI discrimination task, but 8-year-old children scored comparably to the adults. Interestingly, biological motion tasks have been highlighted as potential hallmarks of social cognition abnormal development (Pavlova, 2012).

In previous studies, it was reported that the posterior part of the superior temporal sulcus (pSTS) was commonly activated in response to human motion perception in point-light studies (Bonda *et al.*, 1996; Grossman, 2010; Centelles *et al.*, 2011). In addition, regions that are part of the mirror system network (Rizzolatti and Craighero, 2004) are also recruited when observing human actions. According to the mirror-neuron theory (Rizzolatti and Fabbri-Destro, 2008; Kilner and Lemon, 2013), we simulate the execution of the actions we observe using a system that matches the neural activity produced during action perception and execution. The mirror system network encompasses the posterior parts of the inferior frontal gyri (IFG) (Kilner *et al.*, 2009), the lower parts of the precentral gyri and the supplementary motor area (SMA) and the inferior parietal lobule (Rizzolatti and Craighero, 2004).

Regions associated with the social brain are important to understand the intentions carried by human motions (Saxe, 2006). The social brain is involved in social cognitive process comprehension such as SI (Adolphs, 2009). It encompasses regions that are involved in human motion processing: the posterior temporal cortex, the anterior temporal lobe, the temporoparietal junction, and the medial prefrontal cortex (mPFC) (Van Overwalle, 2009). The pSTS plays a key role in human body perception, in social perception (Lahnakoski *et al.*, 2012), in particular with human motion describing goal-directed actions (Shultz *et al.*, 2011). The social brain is involved in the theory of mind, corresponding to the ability to infer others' mental states such as intentions, beliefs, and desires (Frith and Frith, 2005; Dunbar, 2012).

The concurrent requirement of the social brain and of the mirror neuron systems to understand SIs carried by human motion was revealed in a previous point-light study in adults (Centelles *et al.*, 2011). In addition, regions such as the anterior and posterior STS, the dorso-mPFC (dmPFC), and the IFG are activated to a greater extent when adults are watching realistic videos showing everyday SIs as compared to alone individuals (Iacoboni *et al.*, 2004).

The social brain and mirror systems are of particular interest as they are key to social understanding and they might keep on developing over childhood and adulthood (Grossmann and Johnson, 2007; Kilner and Blakemore, 2007; Shaw and Czekóová, 2013; Soto-Icaza *et al.*, 2015). Indeed, perception and interpretation of SI may evolve throughout development, particularly

during adolescence since changes in terms of relationships and identity occur emerge (Casey *et al.*, 2005; Blakemore, 2010). As social cognitive functions continue to develop over lifespan, cerebral regions go on developing with heterogeneous patterns of gray or white matters volume changes (Gogtay and Thompson, 2010). Indeed, from childhood to adulthood a non-linear decrease in gray matter volume and a linear increase in white matter volume in the frontal and parietal cortices occur (Sowell *et al.*, 1999; Gogtay *et al.*, 2004; Blakemore and Choudhury, 2006). In the frontal lobes, gray matter volume increases until 11 years old before decreasing (Gogtay and Thompson, 2010). Until early adulthood, gray matter volumes decrease in the medial PFC, the pSTS, and the temporo-parietal junction (Mills *et al.*, 2014). This decrease would be mostly explained by synaptic pruning (Blakemore and Choudhury, 2006; Stiles and Jernigan, 2010), even though other mechanisms might occur (such as changes in glial architecture) (Gogtay and Thompson, 2010). Contrary to the sensory and motor brain regions that mature first (Gogtay and Thompson, 2010), synapses rearrangement and myelination continue to develop until puberty in the PFC (Blakemore and Choudhury, 2006). The maturation processes embrace both structural and functional changes during late adolescence and early adulthood (see Cao *et al.*, 2016 for review). These structural maturational mechanisms might contribute to the refinement of brain networks that are involved in more elaborated cognitive processing, such as the fine understanding of subtle SI.

In this study, our aim was to reveal the neural network that supports SI recognition carried by human motion across development. We used point-light displays of human whole-body motion showing people interacting or moving separately. Healthy participants from 8 to 41 years of age performed an SI recognition task with point-light displays, while functional magnetic resonance imaging (fMRI) recorded their cerebral activity. They were separated into three groups: children, adolescents, and adults. Since body language is successfully used to recognize SIs in 8-year-old children (Centelles *et al.*, 2013), we expected similar abilities in the three groups. This ensured possible comparisons between the different age groups as brain activity differences would not be merely sustained by different performance. We expected that the involvement of the social brain and mirror system would be greater in the older groups, as it continues to refine over development, especially during adolescence.

Materials and methods

Participants

Fourteen healthy children (8 females, mean age in years: 9.8 ± 1.0), 14 healthy adolescents (10 females, mean age in years: 14.5 ± 1.0), and 16 healthy adults (8 females, mean age in years: 28.8 ± 7.4) took part in the study. Participants had normal or corrected-to-normal visual acuity and had no significant history of medical, psychiatric, or neurological pathology. None of the participants had previously encountered point-light displays.

Adult participants gave their informed consent, and the children's or adolescent's parents gave their informed consent beforehand. The approval was obtained from the local ethics committee (South Mediterranean 1 Committee for the Protection of Persons).

SI recognition assessment during fMRI acquisition

The task evaluated the ability to recognize SI from point-light displays, with an event-related fMRI design. The set of stimuli

has been described in a study conducted in adults (Centelles *et al.*, 2011) and in a developmental behavioral study (Centelles *et al.*, 2013). Three-second silent videotapes showing two actors performing SI or moving side by side without interacting (NM) were displayed. Markers were taped onto actors' bodies, and the actors' actions were recorded with the SMART automatic motion analyzer. As a result, each actor was depicted by 20 white dots. Motion cues varied with each SI. We tried to render the naturally relevant social motion cues by asking expert actors to perform the screenplays as naturally as possible. The aim was to portray ecological, lifelike everyday social scenes. Stimuli used for SI and NM conditions were matched for overall motion cues and actors' types of movements as closely as possible. The dots were linked by full lines ("stick-lights") in order to simplify the movement perception and explore whether SI would be better recognized with full lines, in particular in the children group. Point-light or stick-light displays enabled the observer to focus on body movements only, without paying attention to other aspects such as facial expressions. Each scene was displayed once with point-lights and once with stick-lights for each participant. We hypothesized that stick-lights would facilitate the recognition of human motion as it easily enables the identification of the shape of the body. Indeed, in a previous study in children aged 4–10 years using the same point-light *vs* stick-light stimuli, a facilitatory effect (decreased response time when children were presented with stick-light stimuli as compared to point-light) had been found (Centelles *et al.*, 2013). Images extracted from the videos showing SI or NM depicted with point-lights or stick-lights are presented in Figure 1. The SI showed either social norms (e.g. handshaking, eight different scenes), games (e.g. playing soccer, seven different scenes), or emotional situations (e.g. frightening someone, five different scenes). The complete description of the stimuli is available in the article by Centelles *et al.* (2013).

One hundred and twelve items showing 20 different SI and 20 different NM were pseudo-randomly presented. It resulted in a presentation of 56 SI and 56 NM scenes, with 28 point-lights displays and 28 stick-lights displays in each category (SI or NM). In half of the SI scenes, the actors were face-to-face, and in the other half, the one was turned sideways with respect to the other. In half of the NM scenes, the two actors were side-by-side, and in the other half the one was turned sideways with respect to the other. They were never presented moving face-to-face in the NM scenes in order to rule out the possibility that their actions might be mistakenly perceived as SIs. The

experiment was divided into four equal runs, each run showing 28 3-second scenes (14 SI and 14 NM). Participants were asked to watch the displays carefully before answering the question "are the two persons acting together or separately?" by pressing one of the buttons, within 3 seconds after the end of the video. During the inter-stimulus interval (3–5 seconds at random, median: 3373 ms), participants looked at a fixation cross on the screen. Participants were asked to answer as spontaneously as possible because the task was timed. No feedback on responses was provided. Participants answered using the index and middle fingers of their right hand to select the left or right answer. Stimuli were presented using a software program based on the LabVIEW 7.1 development system, and responses were recorded with the same software.

Brain activity was measured using the blood oxygen level-dependent (BOLD) contrast with fMRI during the task.

Behavioral data statistics

Performance and response time comparisons between the two categories (SI or NM) were analyzed using a two-way mixed factorial design analysis of variance (ANOVA) with repeated measures, with stimulus type (NM or IS) as a within subject factor, and age group as a between-subject factor. Tukey's post hoc tests were used when applicable. All statistical analyses were performed using R software (http://www.R-project.org), and the threshold for statistical significance was set at $P = 0.05$.

fMRI data acquisition

Images were acquired on a 3-T MEDSPEC 30/80 AVANCE whole-body imager (Bruker, Ettligen, Germany) equipped with a circular polarized head coil.

Anatomical MRI data were acquired using high-resolution structural T1-weighted images (inversion-recovery sequence, resolution $1 \times 0.90 \times 1.42$ mm) in the sagittal plane and covering the whole brain.

Functional images were acquired using a T2*-weighted echo planar sequence covering the whole brain with 32 interleaved 3-mm-thick/1-mm-gap axial slices (repetition time = 2.13 seconds, echo time = 30 ms, flip angle = 79.5°, field of view = 192 mm, 64 × 64 matrix of $3 \times 3 \times 4$ mm voxels). During each run, 137 functional volumes were acquired. Four runs were processed and each run lasted for about 5 minutes.
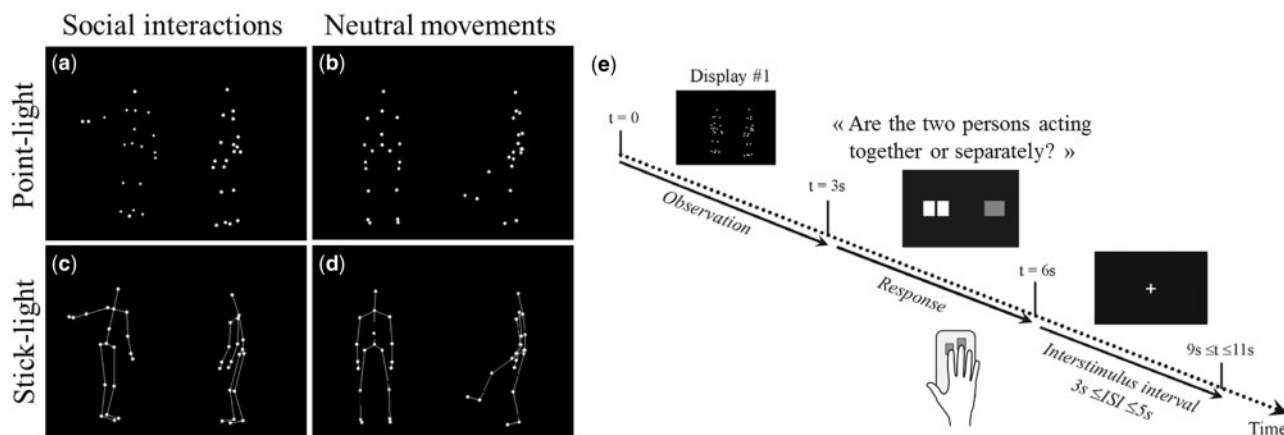

Fig. 1. SI recognition task. Examples of stimuli showing SIs (a, c) or NMs (b, d) with point-light (a, b) or stick-light (c, d) displays during the trial presentation (e).

fMRI processing

All images were preprocessed and analyzed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm) and Matlab R2013a.

Image preprocessing

In each run, the first six functional volumes were removed so as to ensure that longitudinal relaxation time equilibration was achieved. The remaining 131 functional volumes were temporally (slice timing) and spatially (realignment, co-registration, normalization, and smoothing) preprocessed.

Slice time processing corrected differences in image acquisition time between slices, with a halfway acquired slice used as reference. The functional volumes were realigned to remove movement artifact. Runs in which participants had head movements above 3 mm in any direction were discarded (based on the size of one voxel: $3 \times 3 \times 3$ mm). Four children out of the 18 initially recorded were excluded from the analysis since in their case only two runs survived this criterion. Within the remaining participants, two children and one adolescent had one run with head movements over 2 mm (but inferior to 2.5 mm) on the z component in one scan each. All of the participants had four remaining runs, except for two children and two adults for which three runs only could be included in the analysis. Within-subject co-registration registered the functional and anatomical volumes, using the anatomical volume as source image and the mean functional image as reference. The functional and anatomical volumes were then normalized into the standard space of the Montreal Neurological Institute, using the anatomical volume as source image, before being smoothed with a 10-mm Gaussian kernel.

fMRI analysis

The BOLD signal was statistically analyzed with a standard generalized linear model approach, in SPM8. Five regressors were modeled using a 3-second box-car waveform convolved with the canonical hemodynamic response function during the observation of the SI or NM scenes, or during the response period. The four regressors of interest were SI, NM, point-light displays, and stick-light displays. The fifth regressor modeled the 3-second period in which the subjects could give their answer. Considered as an event of no interest, it was nonetheless added to the model to reduce the residual error. Given the high success rate (ranging from 93% to 98%) obtained by the participants during the SI and NM trials, accurately and inaccurately identified scenes were pooled together. Furthermore, we did not want to exclude possible trials where a social scene was indeed perceived and processed as such despite an inaccurate answer.

The first-level *t*-test was performed with a 120-second high-pass filter and scaling option on global normalization. The first-level *t*-test resulted in contrast images that were included in a second-level *t*-test, so as to account for inter-subject variability. Participants were combined as a random factor in the second-level analysis. The factor corresponding to each category of stimuli (SI, NM, stick-lights, and point-lights) was a fixed factor. The (SI > NM) contrast was studied in each group, by comparing the mean of the contrasts across subjects to 0 using a one-sample Student's *t*-test. We first performed an ANOVA to study the effect of the age groups (three levels) on the [SI > NM] contrast. The children, adolescent, and adult groups were then compared with two-sample *t*-tests on the same contrast. In addition, the (stick-light > point-light) contrast was studied in each group (Supplementary data).

To enable a comprehensive overview of the findings, we present the results with two thresholds of correction: a peak-level correction to allow comparisons with a previous fMRI study performed in adults (Centelles *et al.*, 2011), and a cluster-level extent correction. At the peak-level, statistical significance was set at $P = 0.001_{uncorrected}$, with an extent threshold of 10 voxels (based on Centelles *et al.*, 2011). In addition, we indicate when the increased activations remained significant with the cluster-level extent threshold for different P values, and after correction for multiple comparisons using the family wise error (FWE) correction implemented in SPM8.

We performed a second analysis where the three groups were pooled together, and where we used the same parameters as in the analysis described above. In this analysis, age was used as covariate so as to study the effect of age on the contrast (SI > NM).

Results

Behavioral performance

Participants' performance and response times are presented in Figure 2. On average, children failed to answer in 0.4% of the trials, whereas adolescents and adults both failed to answer in 0.1% of the trials.

On average, all three groups successfully performed the SI recognition task: the rate of correct answers reached 93.0% (± 3.4) in the children group, 97.3% (± 1.7) in the adolescent group. The three groups answered as quickly in the SI as in the NM conditions.

Since no differences were found between stick-light and point-light displays within each group, these two presentations were combined in the between-group the analysis.

Comparisons between the three groups

Significant main effects of group on performance ($F(2,41)=5.23$; $P=0.02$) and on response times for correct answers ($F(2,41) = 13.15$; $P < 0.001$) were found. There was no significant effect of the stimulus category (SI or NM) on performance or response time and no interaction between the stimulus category and the group on these variables. Tukey's post hoc tests revealed that children performed worse than adolescents (93% *vs* 97% of correct answers; $P < 10^{-4}$) and adults (93% *vs* 98% of correct answers; $P < 10^{-5}$). Children answered slower than adolescents (1048 *vs* 798 ms; $P < 0.001^{-3}$) and adults (1048 *vs* 726 ms; $P < 10^{-5}$).

Functional imaging correlates

Group analysis. Watching SI in contrast to NM activated a pattern of brain regions presented in Figure 3. The three groups showed activation in the pSTS, in the anterior and posterior parts of the MTG, in the middle occipital gyri (MOG), in the ITG and in the IFG ($P < 0.001_{uncorrected}$).

After FWE correction at the cluster level, children showed activation in the right posterior ITG, the and the bilateral pMTG/pSTS, and the left inferior and MOG. In the adolescent group, activation was found in the bilateral pMTG/pSTS, in the right anterior MTG, in the bilateral MOG and in the bilateral IFG. Finally, the adult group demonstrated activations in the bilateral pMTG/pSTS, in the bilateral IFG, in the left dorsomedial PFC, and in the bilateral caudate nucleus.
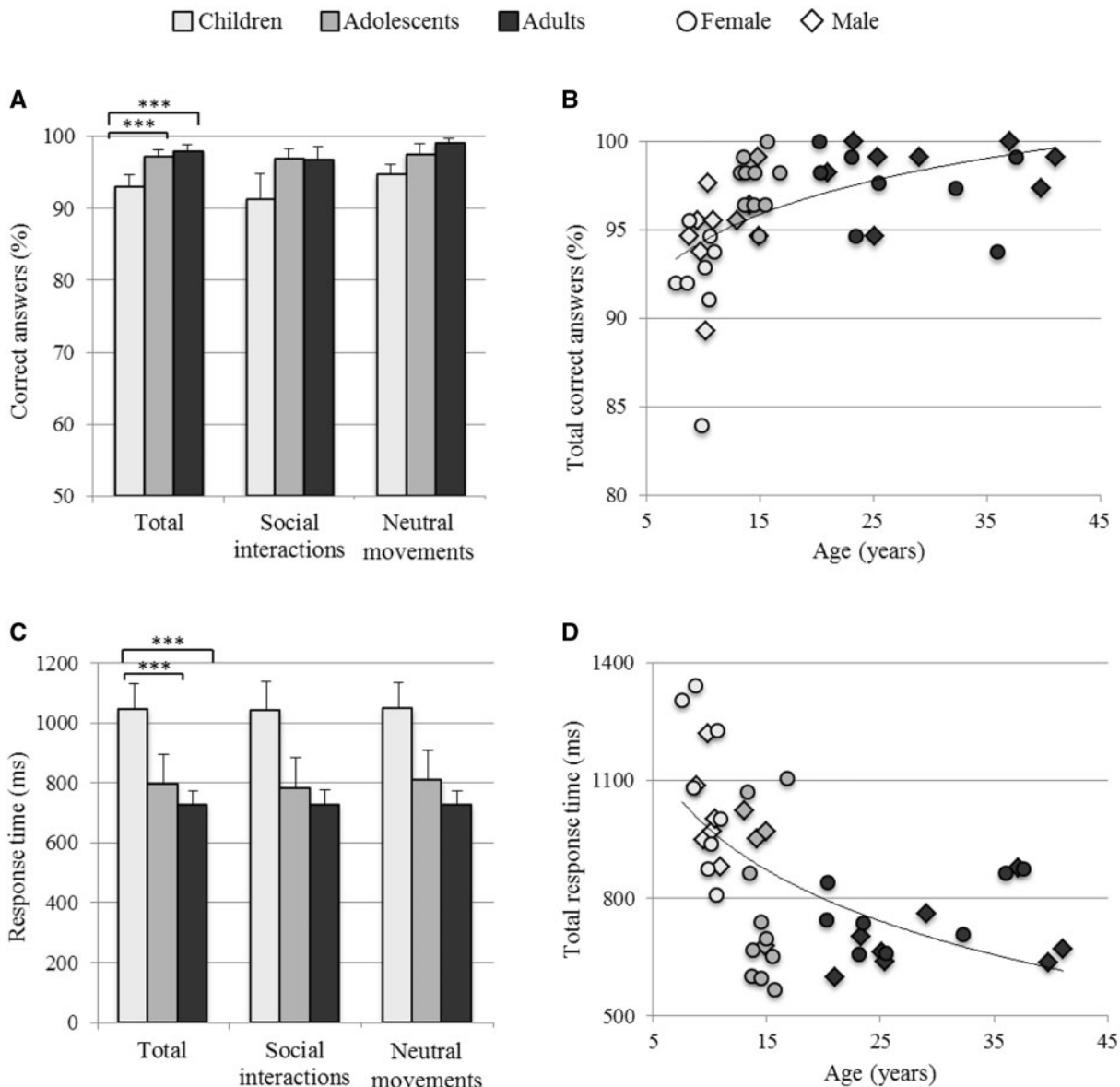
Fig. 2. Performance and response times in the SI recognition task. A and B, Mean percentage of correct answers in total, for the SI scenes and for the NM scenes of the SI recognition task. C and D, Mean response times (ms) for correct answers in total (SI and NM scenes), for the SI scenes and for the NM scenes of the SI recognition task. The two plots (B and D) correspond to the individual total performance and response times (SI and NM scenes) in the SI recognition task (left sections of the A and C histograms). *$P < 0.05$, ** $P < 0.005$, ***$P < 0.0005$. Error bars indicate the s.d.

The group analysis for the contrast NM > SI and the contrast stick-lights > point-lights is described in the Supplementary SI-1 and SI-2, respectively.

Comparisons between the three groups. Figure 4 presents the group comparison results showing regions activated during SI observation in contrast to NM ($P < 0.001_{\text{uncorrected}}$). All of the regions listed in this table were also revealed in the main group effect of the ANOVA for the contrast SI > NM (Supplementary SI-3).

The left angular gyrus and inferior parietal gyrus were more activated in adults than in children when they were watching SI in contrast to NM. No significant differences were found between the children and the adolescent groups.

When watching SI in contrast to NM, adolescents showed greater bilateral activations in the pMTG, pSTS, and MOG than

adults. In contrast, adults showed greater activation than adolescents in the frontoparietal regions: in the dorsolateral and medial parts of the PFC, the middle frontal gyri, the right anterior cingulate gyrus (ACG), the left precuneus, and the angular gyri. Only the increased activation in the pMTG/pSTS cluster in the adolescents as compared to the adults remained significant after FWE correction ($P = 0.02$). However, greater activations in frontal and parietal regions in the adults as compared to adolescents remained close to the significance threshold after FWE correction (e.g. left precuneus: $P = 0.06$, dmPFC cluster: $P = 0.07$; Figure 4).

SIs vs NMs: correlations with age. The analysis using age as covariate revealed almost the same regions as the in-between group analysis (Supplementary SI-4). When watching SI in contrast to NM, some frontal and parietal regions showed increased

Cluster size	Side	Brain region	MNI coordinates x	y	z	T-value
CHILDREN						
341***	R	Inferior temporal g., *post. part*	48	-56	-6	9.4
			45	-44	-18	7.6
	R	Middle temporal g., *post. part*	63	-64	10	6.3
44*	R	Middle temporal gyrus, *ante. part*	54	-8	-18	7.8
283***	L	Middle temporal g./STS, *post. part*	-48	-64	14	7.7
	L	Inferior occipital g./Middle occipital g.	-51	-76	-6	7.4
	L	Middle temporal g., *post. part*	-54	-56	18	6.2
10	R	Fusiform g.	-36	-48	-14	4.9
39*	L	Inferior frontal g., *opercular part*	-51	8	26	5.4
33*	R	Inferior frontal g., *triangular part*	51	24	14	5.2
			51	16	22	4.9
17	R	Insula, *ante. part*	33	28	-2	5.0
ADOLESCENTS						
370***	L	Middle temporal g./STS, *post. part*	-54	-60	14	10.7
	L	Middle occipital g.	-36	-84	18	9.3
	L	Inferior occipital g.	-39	-72	-10	4.5
688***	R	Middle temporal g., *ante. part*	51	4	-26	10.2
	R	Superior temporal sulcus, *post. part*	48	-32	-2	9.8
	R	Middle occipital g.	33	-80	6	8.4
35*	L	Fusiform g.	-45	-56	-22	5.3
			-42	-48	-22	5.0
113***	L	Inferior frontal g., *orbital part*	-39	24	-10	8.0
			-36	24	-18	6.5
			-51	20	-6	6.2
70**	L	Inferior frontal g., *opercular part*	-54	16	18	5.7
	L	Inferior frontal g., *triangular part*	-57	20	26	5.5
100***	R	Inferior frontal g., *triangular part*	57	24	2	6.4
			57	16	22	5.3
20*	R	Precentral g.	48	-8	54	6.1
22*	L	Precentral g.	-45	0	54	6.3
			-51	4	46	5.3
40**	R	Supplementary motor area	6	12	62	6.9
19	R	Superior parietal g.	30	-52	58	5.1
12	R	Caudate nucleus	15	8	10	6.1
ADULTS						
163***	L	Middle temporal g./STS, *post. part*	-45	-56	10	7.7
			-45	-64	14	7.3
			-60	-52	-2	4.4
24*	R	Inferior temporal g., *post. part*	45	-44	-18	6.0
76***	R	Inferior temporal g., *post. part*	60	-64	6	5.6
	R	Middle occipital g.	39	-72	22	5.0
	R	Middle temporal g., *post. part*	51	-72	14	4.7
24*	R	Middle temporal g., *ante. part*	51	16	-30	6.7
33*	L	Inferior temporal g., *post. part*	-42	-48	-18	5.3
198***	L	Inferior frontal g., *triangular part*	-57	24	14	7.6
	L	Inferior frontal g., *orbital part*	-27	28	-14	7.0
			-45	32	-10	5.0
44**	R	Inferior frontal g., *triangular part*	57	24	10	6.2
			54	32	-2	5.4
15	L	Precentral g.	-51	0	42	4.5
8 svc	L	Supplementary motor area	0	16	58	4.3
51**	L	Superior frontal g., *dorsomedial part*	-6	52	38	7.3
25*	R	Superior parietal g.	18	-64	66	5.3
30*	L	Superior parietal g.	-30	-64	66	5.3
			-39	-60	62	4.5
123***	R	Caudate nucleus	9	12	6	6.7
	L	Caudate nucleus	-6	8	6	6.5

Fig. 3. Brain regions showing increased activity in response to the SI observation than NM observation in the children, adolescent and adult groups. Significance threshold was set at $P < 0.001_{uncorrected}$ at the peak level. The level of significance at the cluster level is indicated with an asterisk following the cluster size (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ at the cluster level). Regions without any sign correspond to the ones only significant at the peak level ($P < 0.001_{uncorrected}$). Regions whose names are written in bold correspond to the regions remaining significant after FWE correction at the cluster level. Regions that remained significant after FWE rate correction at the peak level are reported with an asterisk following the T-value, and at the cluster level with a sharp sign following the cluster size. SVC: Small volume correction based on previous results (Centelles *et al.*, 2011). In the first column, blue corresponds to the temporal and occipital lobes, red corresponds to the frontal and parietal lobes, grey to the insular lobe, and green to the caudate nucleus. Regions activated in all three groups are in bold. L/R: left/right; g: gyrus.
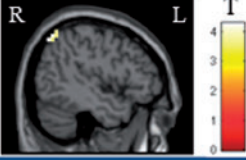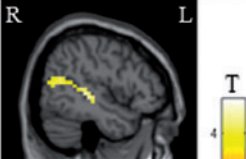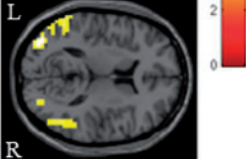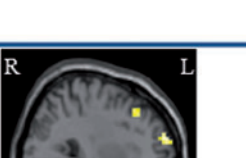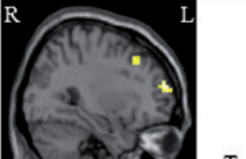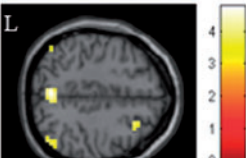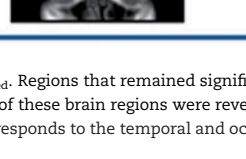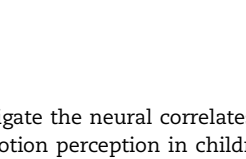
Cluster size	Side	Brain region	MNI coordinates x	y	z	T-value	
ADULTS > CHILDREN							
14	L	Angular g.	-45	-68	50	4.3	
	L	Inferior parietal lobe	-48	-60	54	4.3	
ADOLESCENTS > ADULTS							
68**	**R**	**Middle temporal g./STS,** *post. part*	48	-32	2	4.7	
			48	-60	18	4.2	
			48	-68	14	4.0	
37*	L	Middle temporal g./STS, *post. part*	-54	-56	14	4.2	
			-63	-52	14	4.2	
			-54	-68	18	4.0	
41*	L	Middle occipital g.	-39	-80	14	5.2	
10	R	Middle occipital g.	27	-84	14	4.0	
ADULTS > ADOLESCENTS							
44*	L	Superior frontal g., *dorsolateral part*	-21	60	22	4.6	
	L	Middle frontal g.	-24	52	10	4.4	
	L	Superior frontal g., *dorsomedial part*	-12	48	6	3.8	
21	L	Superior frontal g., *dorsolateral part*	-18	36	38	4.3	
32*	R	Superior frontal g., *dorsolateral part*	27	60	18	4.4	
			18	68	10	3.6	
11	R	Middle frontal g.	27	32	42	3.9	
10	R	Anterior cingulate g.	15	44	6	3.8	
	R	Superior frontal g., *medial orbital*	6	48	-2	3.6	
46**	L	Precuneus	-3	-68	46	4.7	
			-12	-60	34	4.4	
13	L	Angular g.	-45	-68	50	4.8	
15	R	Angular g.	45	-60	42	3.8	
			45	-72	46	3.8	

Fig. 4. Group comparison: regions showing greater activation for SIs than NMs. Significance threshold was set at $P < 0.001_{uncorrected}$. Regions that remained significant at the cluster level are reported with an asterisk following the cluster size (*$P < 0.05$, **$P < 0.01$, name in bold: FWE correction). All of these brain regions were revealed in the analysis (ANOVA) of the main age group effect on the contrast SIs > NMs (Supplementary SI-3). In the first column, blue corresponds to the temporal and occipital lobes, and red corresponds to the frontal and parietal lobes. L/R: left/right. g: gyrus.

activation with age, whereas temporal and occipital regions showed decreased activation with age. Indeed, with increasing age, greater activations were found in the middle frontal gyri, the ACG, the SMA, the precuneus, the inferior parietal lobe (IPL), the angular gyrus, and the cerebellum. With decreasing age, greater activations were found in the posterior parts of the ITG, MTG, and STS, as well as in the inferior and MOG and in the calcarine fissure.

Discussion

This study was designed to investigate the neural correlates of SI recognition based on human motion perception in children, adolescents, and adults. The three groups successfully identified the scenes showing people interacting, even though the children had a slightly lower performance and answered more slowly. The stimuli were chosen to be easy to categorize as the

recognition accuracy should not differ much between the three groups in order to be comparable in terms of social recognition level, hence enabling the comparison of brain activity. The main activations in response to the recognition of SIs based on human motion perception were found in the IFG, the anterior temporal lobes, and a large cluster in the pSTS area stretching from the posterior ITG to the MOG. Our major results are summarized in Figure 5. They suggest that interestingly, a set of core regions enabling the discrimination of SIs from NMs overlapped in the three groups. These regions would allow a general understanding of SIs during non-verbal communication. The recruitment and differentiation of an additional set of regions in the two older groups would enhance the ability to grasp subtle kinematic cues and interpret their meaning in the context of SIs.

Human motion is sufficient to recognize SIs

The experimental procedure used in the present study made it possible to specifically isolate the social content carried by whole-body movements. Consistently with previous findings (Centelles *et al.*, 2013), we found that individuals from 8 years of age were able to use cues from minimalistic presentations of human motion to determine whether people were interacting. We did not find any facilitator effect related to stick-light

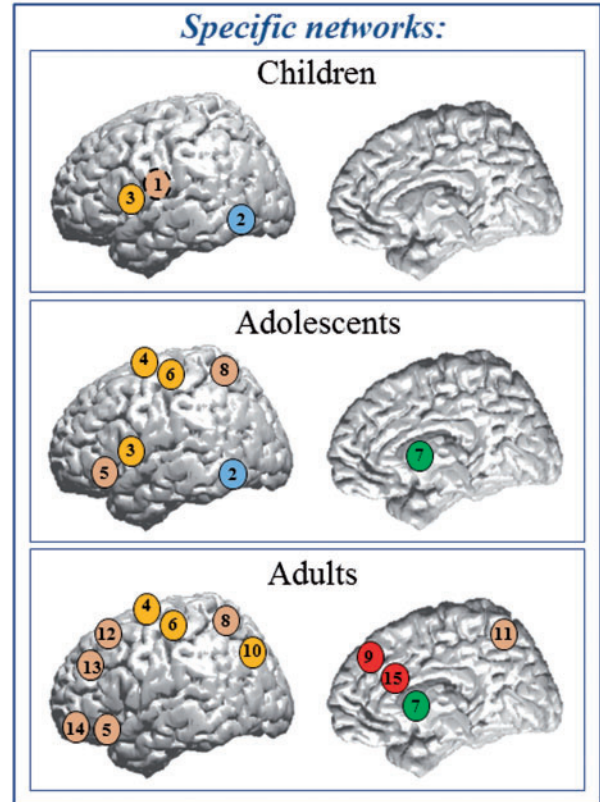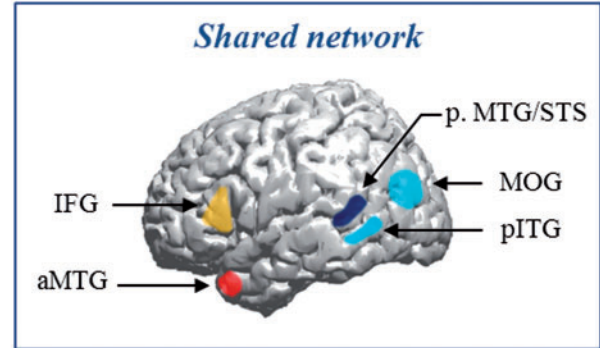| n°	Regions	Literature		Results		
		HM	SI	Children	Ado.	Adults
1	Insula					
2	Fusiform g.	✓	✓		+	
3	IFG *opercularis*	✓	✓	+	+	
•	pMTG / pSTS	✓	✓	+	+×	+
•	pITG	✓	✓	+	+	+
•	aMTG			+	+	+
•	IFG *triangularis*		✓	+	+	+
•	MOG			+	+×	+
4	SMA				+	
5	IFG *orbital*		✓		+	+
6	Precentral g.				+	
7	Caudate nucleus					+
8	Sup. parietal g.		✓			+
9	dm PFC		✓			+×
10	IPL, angular g.					×
11	Precuneus		✓			×
12	dl PFC					×
13	Medial frontal g					×
14	Orbital PFC					×
15	ACG					×

Fig. 5. Neural correlates of social interaction recognition across development. This figure summarizes the group analysis results of the fMRI study, in the children, adolescent and adult groups. The table (left) describes the regions activated during the observation of SI *vs* NM in our study, and the findings from other studies: activation during human motion (HM) or SI observations. At the group level, regions which showed increased activation for SI > NM are indicated in color, and with a "+" for when remaining significant at the cluster level. The "x" sign indicates the regions revealed in the group comparison for the contrast SI > NM. The illustrations (right) present the networks shared by the three groups (top panel) and regions specific to each group. Numbers correspond to the regions indicated in the table. The brain regions involved in visual perception are represented in light blue, in the mirror system in yellow, in the social brain in red, and regions involved in these three networks are in dark blue. The caudate nucleus is indicated in green, and other regions are represented with brown color. g.: gyrus, sup.: superior, Ado.: adolescents.

presentation as compared to point-light, probably because children from the current study were older in average. This result might be quite surprising since the ability to integrate local motion signals into a global flow of motion follows a long developmental trajectory until 12 to 14 years of age (Hadad et al., 2011). Yet, compared to the older groups, the children showed slightly reduced abilities to understand human motion in the task, even though they reached very good performance (93% of correct answers).

Moreover, the cognitive abilities necessary for subtle SI recognition based on human motion perception seem to be well developed in adolescents, since they performed as quickly and as accurately as adults. In adolescents, an action representation system must be already acquired, but must continue to refine during adolescence (Choudhury et al., 2007).

Core regions for SI understanding

We characterized a network involved in SI recognition, which was shared by the three groups. It encompasses regions involved in human motion processing, in the mirror network, and in the social brain. This network reflects SI discrimination based on human motion mainly. However, we cannot rule out the possibility that spatial judgment processes might have been at work as well, as the position of the two actors could also indicate whether they were interacting or not. Indeed, the actors were sometimes facing each other during SIs, while they were never face-to-face when acting separately.

Human motion processing. Body motion is perceived in the visual areas of the occipital lobe (particularly in V5), before being processed by the ITS and pSTS (Decety and Grèzes, 1999). Congruently, the MOG, ITG, and pSTS were identified in all three groups. Investigation about the pSTS revealed its specialization in body motion perception with point-light displays (Beauchamp et al., 2003; Saxe, 2006; Grossman, 2010), in SI perception (Schultz et al., 2005; Centelles et al., 2011; Gao et al., 2012), as well as in the perception of actions directed toward a goal (Saxe et al., 2004). In addition, reading stories depicting biological motion also activated the pSTS, the ventral temporal areas, the precuneus, and the premotor and motor cortices (Deen and McCarthy, 2010). Lesions in the superior temporal and premotor areas lead to impaired recognition of biological motion displayed with point-lights (Saygin, 2007). Despite the late maturation of the STS (Gogtay and Thompson, 2010), this region was recruited in the three groups during the analysis of human motion showing SI. The pITS, the fusiform gyri, the premotor cortices, the IFG opercular, and the inferior occipital gyri are also involved in biological motion perception (Grossman, 2010; Herrington et al., 2011).

The presentation of SI through human motion activated the dmPFC, the IFG, the fusiform gyri, and the precuneus, as in the study by Iacoboni et al. (2004) where realistic SI were shown. The information carried by human motion only is thus sufficient to activate the regions involved in the observation of realistic SIs. Moreover, the network identified during SI observation was quite similar to the one recruited during the observation of pictures depicting cooperative SI (Canessa et al., 2012): the orbital gyri, IFG, medial PFC, fusiform gyri, ITG, MTG, precuneus, and superior parietal gyri. There might, therefore, be a common neural basis involved in the perception of SI depicting games, emotional situations, social norms, or cooperation. This brain network would be activated not only by realistic videos depicting SIs but also by minimalistic information carried by human motion and even by static pictures depicting SI.

Mirror neuron system. During SI observation based on human motion, greater activations in the IFG and STS were found. As a part of the mirror system, these regions contribute to internally simulate the observed action. Since SI depicted more complex and more meaningful actions than NM, it might explain the greater recruitment of the mirror system in this condition.

Other regions, which are parts of the mirror network, were also recruited: the precentral gyri and the SMA in the adolescent and adult groups and the IPL in the adult group. In contrast, these regions may not have shown increased activation in the children either because some SIs were not part of their motor repertoire yet or because their mirror system was less refined. Indeed, according to a developmental account of the mirror neuron system function, it is forged by sensori-motor experience in the course of individual development (Heyes, 2013; Cook et al., 2014).

Social brain network. In all three groups, we found activations in the anterior MTG during SI observation, which is a part of the social brain. We also found that regions of the social brain (dmPFC and ACG) were more activated in the adult group, consistently with studies indicating that adults recruit regions from both the mirror system and social brain to recognize SIs (Centelles et al., 2011).

Participants probably tried to infer the story created around the scene so as to make their decision and indicate whether it was a SI or NM scene. The SI scenes varied in complexity: it might have been easy to understand that the two individuals were hand-shaking, whereas it might have needed more mentalizing processes to occur to understand that two individuals were moving their arms to express their happiness when meeting up. However, since the scenes were displayed for 3 seconds only, they did not have time to create very complex or detailed story around it.

Additional regions and refinements across development

Activations in regions involved in human motion processing (pSTS/pMTG and MOG) were present in the three groups. However, surprisingly, adolescents showed greater activation in these regions than adults. The temporal lobes undergo a strong age-related increase in lobar white matter, a maturational process that is consistent with progressive myelination (Brain Development Cooperative Group, 2012). Interestingly, the pSTS might also show different maturational processes depending on which side. A longitudinal study in adolescents performing a mentalizing task has revealed that while activations in the right pSTS show stability over time, the left pSTS on the other hand shows a dip in mid-adolescence (Overgaauw et al., 2015).

Adults recruited frontoparietal regions part of the mirror system or to the social brain to a greater extent than adolescents. It suggests that the social brain and mirror system continue to develop and to refine over development. Contrary to the younger groups, which tended to use occipito-temporal regions to a larger extent, the older groups required more frontoparietal regions to analyze SIs. To investigate SI scenes, brain regions involved in visual perception were recruited to a greater extent in children, whereas regions involved in the interpretation of the SI meaning were recruited to a greater extent in adults. The level of social understanding of the displayed situation might have influenced the brain activity while performing

the task. Indeed, the increased activation in regions of the social brain or mirror neurons in the older groups might be due to the fact that they were grasping the complete meaning of the SI. Children might have sometimes felt that the persons were interacting without perceiving the exact meaning of the situation. Hence, different levels of understanding might explain differences in the level of activation within the involved brain regions in the three age groups.

The lack of significant brain activity differences we found when comparing the older groups to the children might be caused by the broader activity dispersion of the latter. This dispersion may be due to the sample effect or may reflect the ongoing brain maturation characterized by lower specificity in the neural circuitry. A limitation to the group comparison is that after FWE correction, only the increased activation in the MTG/pSTS cluster in the adolescent group as compared to the adult group remained significant. However, in adults other frontal and parietal regions (e.g. the dmPFC and the left precuneus respectively) showed greater activity close to the significance threshold after FWE correction.

Caudate nucleus in the older groups. In the adolescent and adult groups only, activation was found in the caudate nucleus in response to SIs. Increased activity of the caudate nucleus has been previously found when watching human motion depicted by point-lights, either when compared to random motion (Bonda *et al.*, 1996) or when observing a SI scene as compared to NMs (Centelles *et al.*, 2011). The caudate nucleus is a region classically involved in motor processing, but it is also central to more cognitive functions. In particular, it has been involved in social decoding processes such as emotion recognition and theory of mind (Kemp *et al.*, 2013). In our study, the SIs scenes encompass emotional situations, and call for theory of mind processing as compared to NMs, therefore producing more activation in this region. Interestingly, while an increased activity was found in the caudate nucleus both in adults and adolescents during the social scenes, children did not show any greater activation. They uniquely presented with increased activity in the insula, an emotive region that would also be activated in competitions between humans (Polosan *et al.*, 2011). Furthermore, the caudate nucleus has been involved in social state encoding. A study in monkeys revealed two groups of neurons in the caudate nucleus: one responding to reward expectation and another encoding social state information (dominant/submissive) (Santos *et al.*, 2012). In our study, SIs were defined as depicting an agent initiating the action and the other agent reacting to this action, which can be interpreted as a dominant/submissive hierarchy. This is even more obvious for the SIs that depicted social conventions, or when the action of the first actor induced an emotional state in the other. Unlike the adolescents and adults, the children might not have grasped subtle social hierarchical links between the two actors, hence the lack of activation in the caudate nucleus.

Brain regions specific to adults. The precuneus was more activated in adults than in adolescents. This region is involved in a wide range of process, but interestingly it shows increased activity in tasks involving first-person perspective taking related to the experience of agency (Cavanna and Trimble, 2006). However, increased activation of the precuneus during third-person observation was also found and is supported by the hypothesis that overactivation of regions involved in self-representation occurs during the third-person perspective simulation because the brain creates a particularly vivid

representation of the self in order to be able to imagine another person with the same neural resources as the self (Ruby and Decety, 2001). Indeed, adults might have imagined themselves performing the action from a first-person perspective to interpret the observed SI scene, to a greater extent than the younger groups. Interestingly, a study by Cavanna and Trimble (2006) showed a connection between the precuneus and most of the regions revealed in the adult group: the SMA, the caudate nucleus, the superior parietal gyrus, the IPL, the dorsolateral PFC, and the ACG. The precuneus might thus play a major role in the developing network involved in SI recognition.

In addition, the dmPFC, was recruited by adults to a greater extent than in adolescents. The dmPFC plays an important role both in inferring mental states and in discriminating SIs. In terms of development, the PFC has been classically found to keep on developing during adolescence, whereas other brain regions have almost reached their final maturation (Casey *et al.*, 2005; Gogtay and Thompson, 2010; Blakemore, 2012). After puberty, synapses of the PFC undergo pruning (Blakemore and Choudhury, 2006), leading to increased signal-to-noise ratio and specialized regions. Activation might then be more easily detectable and the maturation process could result in increased efficiency and reactivity (due to automatic circuitry), explaining its increased activation in adults.

Conclusions

Children, adolescents, and adults managed to identify SI based on human motion information only. Watching SIs led to the activation of the same brain regions in all three age groups, showing stability of these regions over time (IFG, aMTG, pSTS/MTG, pITG, and MOG). Additional brain regions were recruited in the older groups, in particular, regions that are part of the social brain and of the mirror system. The developmental changes found in this study may result from gray matter maturation, new anatomical connections, and refinements in the social brain and mirror system. Further functional connectivity studies would provide interesting information on the functional networks involved in SI recognition. This study sets the basis for the typical development of the networks involved in SI understanding during non-verbal communication. It would be interesting to study the development of these networks in situations of atypical development of social cognitive processes, as encountered in autism spectrum disorders.

Supplementary data

Supplementary data are available at *SCAN* online.

Conflict of interest. None declared.

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