

The neural basis of the imitation drive

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Abstract

Spontaneous imitation is assumed to underlie the acquisition of important skills by infants, including language and social interaction. In this study, functional magnetic resonance imaging (fMRI) was used to examine the neural basis of ‘spontaneously’ driven imitation, which has not yet been fully investigated. Healthy participants were presented with movie clips of meaningless bimanual actions and instructed to observe and imitate them during an fMRI scan. The participants were subsequently shown the movie clips again and asked to evaluate the strength of their ‘urge to imitate’ (Urge) for each action. We searched for cortical areas where the degree of activation positively correlated with Urge scores; significant positive correlations were observed in the right supplementary motor area (SMA) and bilateral midcingulate cortex (MCC) under the imitation condition. These areas were not explained by explicit reasons for imitation or the kinematic characteristics of the actions. Previous studies performed in monkeys and humans have implicated the SMA and MCC/caudal cingulate zone in voluntary actions. This study also confirmed the functional connectivity between Urge and imitation performance using a psychophysiological interaction analysis. Thus, our findings reveal the critical neural components that underlie spontaneous imitation and provide possible reasons why infants imitate spontaneously.

Key words: spontaneous; imitation; urge; mirror neuron; autism

Introduction

One key question regarding the mechanisms underlying human imitation is why infants spontaneously imitate the unfamiliar

actions of others without being asked to do so. Spontaneous imitation is assumed to support the acquisition of important skills in infants, including language (Kuhl and Meltzoff, 1996),

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tool use (Abravanel et al., 1976) and social interaction (Chartrand and Bargh, 1999; Lakin and Chartrand, 2003; Meltzoff and Decety, 2003). The innate nature of the ability to engage in spontaneous imitation is suggested by the existence of this ability in human neonates (Meltzoff and Moore, 1977, 1983) and neonatal chimpanzees (Myowa-Yamakoshi et al., 2004; Ferrari et al., 2006). In humans, spontaneous imitation of simple body movements is initially observed during the first 2 years after birth, when infants develop their primal instincts and are most dependent on their parents (Piaget, 1962, 1983; Meltzoff, 1990). However, infants and children with autism spectrum disorders (ASDs) display less imitation compared with typically developing children, suggesting that a deficit in this ability may be associated with insufficient development of social skills and language in children with these disorders (Williams et al., 2004; Hamilton, 2008; De Giacomo et al., 2009; Lai et al., 2013).

Two distinct processes should be considered with respect to the cognitive processes underlying spontaneous imitation: the process that enables the performance of imitation *per se*, which is recruited regardless of whether the imitation is spontaneous, and the process that drives imitation, which is more relevant to the issue of why infants 'spontaneously' imitate. These two processes were identified as distinct using recently proposed multi-component models of imitation (Brass and Heyes, 2005; Rumiaty et al., 2005; Brugger et al., 2007; Lestou et al., 2008; Southgate and Hamilton, 2008; Catmur et al., 2009).

Previous neuroimaging studies have generally investigated the neural basis of imitation performance. Earlier studies (Iacoboni et al., 1999, 2001; Nishitani and Hari, 2002) are likely to have been motivated largely by the concept of mirror neurons (MNs), which discharge during the observation and execution of an action (Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004). This common coding has typically been associated with activation in the inferior and superior parietal lobules, as well as the dorsal and ventral premotor cortices (Iacoboni et al., 1999; Buccino et al., 2004; Vogt et al., 2007). However, some of these observations (e.g. Broca's area) may not be related to the neural processes crucial to imitation itself (Rushworth et al. 2001a; Makuuchi, 2005).

In this study, functional magnetic resonance imaging (fMRI) was used to examine neural correlates of the imitation drive, which have not yet been fully investigated. More specifically, this study investigated the driving process that is activated when humans spontaneously try to imitate an unfamiliar action without explicit reasons. To achieve this, meaningless actions were prepared, and the 'urge to imitate' (Urge) was defined as a means of measuring the imitation drive. Two potential confounding factors were given particular attention during the isolation of neural correlates underlying Urge. First, in adult participants, the urge to imitate can result from explicit reasons, which may include the fact that the presented action appears familiar, challenging or interesting. Thus, attempts were made to eliminate the effects of these types of upstream cognitive processes on imitation drive by creating a questionnaire to evaluate the potential involvement of these explicit reasons and the strength of the urge to imitate. Second, the strength of the urge to imitate may be correlated with various kinematic characteristics of the perceived action, including perceptual factors such as speed or complexity. Therefore, various types of kinematic factors were included in the stimuli set, and neural correlates of the imitation drive were assessed using *post hoc* multiple regression analyses. To determine the brain regions associated with imitation drive, the cortical areas in

which the degree of activation was positively correlated with Urge score were determined. Finally, in addition to identifying areas that positively correlated with Urge, the neural networks underlying Urge and imitation performance were also assessed using a psychophysiological interaction (PPI) analysis to confirm functional connectivity between these two factors.

Materials and methods

Participants

Forty-two healthy, right-handed participants with no psychiatric or neurological history were evaluated. The data from five participants were excluded from the final analyses due to excessive head motion (>2.5 mm; $n=2$) or non-compliance with task instructions (two participants made mistakes on the rating, and one participant imitated all actions during the observation condition even though he understood the instructions). Thus, data from the remaining 37 participants (mean age 20.8 ± 1.5 years; range 18–25 years; 23 males and 14 females) are reported. Handedness was evaluated using the Edinburgh Handedness Inventory (Oldfield, 1971). Informed consent was obtained from all participants prior to their participation. This study was approved by the Ethics Committee of Tohoku University Graduate School of Medicine.

Stimuli

A total of 106 cyclic bimanual actions were identified as candidate actions for the stimuli. The cycle speed was the same for every action and maintained using a metronome ($\text{♩}=96$). Each action was repeated twice and the stimulus movie clip was 5 s in duration. We prepared 106 original movie clips as well as double-speed versions of the original clips using video editing software (Premiere Pro CS4, Adobe Systems, Inc., San Jose, CA, USA). Each movie was clipped to a 5-s duration; therefore, a total of 212 movie clips was prepared. Based on preliminary experiments, we selected 24 movie clips of different meaningless bimanual actions as visual stimuli for our fMRI analysis (Figure 1).

Questionnaire construction and image selection

To create a questionnaire for evaluating the degree of urge and explicit reasons to imitate, we first collected candidate descriptors. Twenty-three healthy participants (mean age 27.1 ± 4.9 years; range 22–31 years; 10 males and 13 females) were asked to imagine situations in which they feel the urge to imitate. Then, factor analysis was performed to construct a questionnaire by determining dominant factors of the 24 descriptors (Supplementary Table S1). Ninety-six healthy participants (mean age 19.3 ± 0.8 years; range 18–22 years; 48 males and 48 females) were shown 13 movie clips of meaningless bimanual actions. Participants rated each movie clip based on the 24 descriptors using a 7-point scale (0—totally disagree; 6—totally agree). After factor analysis, four factors were determined according to Kaiser's criteria (Kaiser, 1960): urge to imitate (Urge), familiarity of the action (Familiarity), apparent difficulty to perform (Difficulty) and rhythmic action (Rhythm). To increase the stability of measurement, two items were selected that showed the largest loadings for Urge: Urge 1, I would like to respond to this person; Urge 2, My hands move almost automatically (or reflexively); Familiarity, I have seen this action many times; Difficulty, The action looks difficult to perform; and Rhythm, The action is rhythmic (Supplementary Table S2). Using the

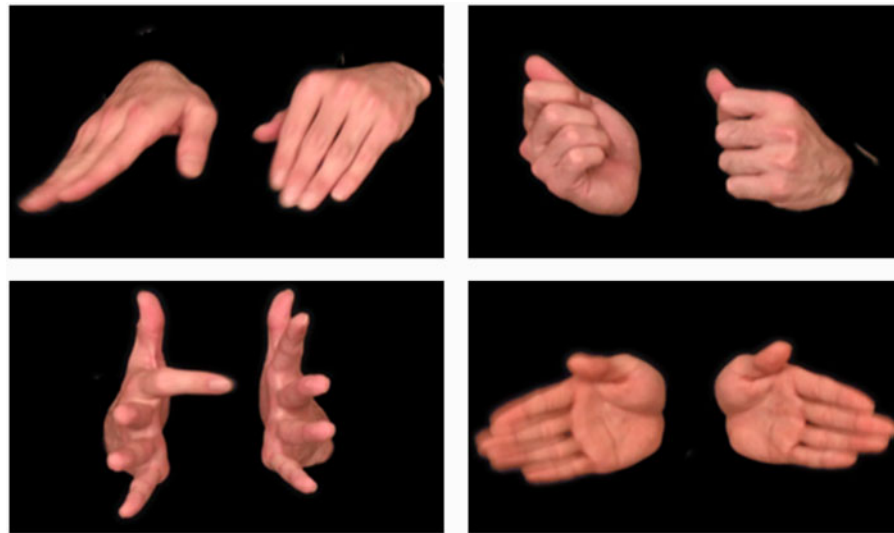


Fig. 1. Examples of stimuli. Clockwise from top left: Snapshots excerpted from movie clips Numbers 1, 2, 11 and 23 (Supplementary Table S3).

constructed questionnaire, we conducted an image selection experiment. Separate stimulus sets were prepared for male and female participants, which involved the showing of hand actions by an actor of the same sex as the subject and included the same set of actions for both genders. A pilot study revealed that some participants felt a gender difference and did not feel the urge to imitate when shown stimuli presented by a person of the opposite sex. Fifty-five participants (mean age 20.6 ± 1.2 years; range 18–23 years; 33 males and 22 females) were shown all candidate movie clips and rated each clip using the questionnaire. As many different kinematic characteristics (speed, key motion, motion type and symmetry) as possible were included in the stimuli to avoid the dependence of Urge on certain kinematic characteristics.

fMRI design

Each subject was asked to lie in supine position on the bed of an MR scanner during the experiment. Participants' hands were fixed at waist level, with their two wrists locked using a soft figure-eight band so that they could imitate the presented action without effort and maintain appropriate joint angles of their shoulders and elbows. The participants wore insulator gloves to prevent any flow of electricity through their body while their hands were touching during the scan. Visual stimuli were projected on the semi-lucent screen placed over the participant's head, and the participant viewed them via a mirror attached to the head coil of the MR scanner. The fMRI design used in this study included two phases within a block: the observation phase and the imitation phase. Participants were instructed to observe an action (observation phase) and then imitate that action (imitation phase) during the fMRI scan. The movie clip presented in each phase was the same. Each phase began with a rest (10.5 s), followed by the instructions (2 s), followed by presentation of the action (10 s). There was a 12.5-s rest break and instruction period between the observation phase and imitation phase. One block lasted a total of 45 s.

Movie clips were presented in pseudorandom order, and the experimental session lasted a total of 18 min and 24 s (Figure 2). Following the fMRI scan, each subject watched the movie clips once again and rated the Urge, Familiarity, Difficulty and Rhythm on a 7-point scale using a laptop in a soundproof room.

fMRI data acquisition

A time-course series of 442 volumes was acquired using T2*-weighted gradient-echo echo-planar imaging (EPI) sequences and a 3-Tesla MR scanner (Achieva Quasar Dual, Philips Medical Systems, Best, The Netherlands). Each volume consisted of 41 transaxial slices covering the entire cerebrum (echo time = 30 ms; flip angle = 85° ; slice thickness = 2.5 mm; gap = 0.5 mm; field of view = 192 mm; 64×64 matrix; voxel dimension = 3.0×3.0 mm) and a repetition time of 2500 ms.

Behavioral data analysis

We investigated the correlation between Urge scores and other confounding factors (i.e. Familiarity, Difficulty and Rhythm scores). First, we calculated correlation coefficients between Urge scores and those of other confounding factors at the individual level. After Fisher's Z transformation, one-sample t-tests was performed and the correlation between Urge scores with other confounding factors was determined.

fMRI data analysis

fMRI data were preprocessed and analyzed using Statistical Parametric Mapping (SPM8) software (Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB R2013b (MathWorks, Natick, MA, USA). As a preprocessing procedure, correction for head motion, slice timing, spatial normalization using the EPI-MNI template and smoothing using a Gaussian kernel with a full-width at half maximum of 6 mm were conducted. A conventional two-level approach for the multi-subject fMRI dataset was adopted. As a first-level within-subject (fixed effects) analysis for parameter estimation, a voxel-by-voxel multiple regression analysis of the expected signal changes was applied to the preprocessed images of each subject. This analysis employed event-related convolution models using the hemodynamic response function provided by SPM8 (Statistical Parametric Mapping, University College London). Two canonical regressors were constructed for each condition (i.e. observation and imitation). The onset and duration of these models were matched to the onset and duration of the movie clip, and therefore, the duration of the predicted blood oxygen level-dependent (BOLD) signal for each condition

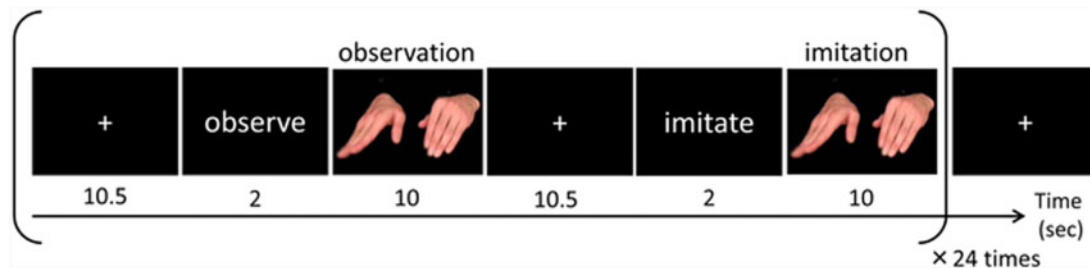


Fig. 2. fMRI design. The fMRI design used in this study included two phases within a block: the observation phase and the imitation phase. The participants were instructed to observe an action (observation phase) and then imitate that action (imitation phase) during the fMRI scan. The movie clip that was presented in each phase was the same. Each phase began with a short rest (10.5 s) followed by the instructions (2 s) and then the presentation of the action (10 s). There was a 12.5-s rest break and instruction period between the observation and the imitation phases. One block lasted a total of 45 s. The movie clips were presented in a pseudorandom order, and the experimental session lasted a total of 18 min and 24 s.

was 10 s. Mistakes made during the observation condition, such as hand movements made by a participant, or during the imitation condition, such as incorrect imitation of the action by a participant, were assigned to a failure block, which was modeled separately and not analyzed further.

Since the neural activations exhibiting amplitudes that were parametrically modulated by action-specific parameters (i.e. Urge and other confounding factors) were of particular interest, parametric modulation analyses were implemented in SPM8, which implements not only canonical regressors to the model mean response for each phase, but also parametric regressors to model modulation during the responses that correlated with parameter. Four parametric modulation models corresponding to the four parameters used to investigate modulatory effects were constructed, and therefore, the five regressors were set up in a design matrix (Observation-canonical, Observation-parametric, Imitation-canonical, Imitation-parametric and Failure-canonical) for each parameter. To remove the artifacts generated by head motions during imaging, estimated motion parameters of six columns were entered in the first level.

The statistical inference of parameter estimates in the parametrically modulated model was performed with a second-level between-participants (random effects) model using a one-sample *t*-test. Brain regions in which the degree of activation was positively correlated (i.e. positive parameter estimate or positive slope of the regression line) with participant-specific and action-specific scores for Urge and other confounding factors (i.e. Familiarity, Difficulty and Rhythm) were identified separately for observation and imitation conditions. The statistical threshold was set to $P < 0.001$ and corrected to $P < 0.05$ for multiple comparisons using cluster size (Friston et al., 1996).

The primary purpose of this study was to clarify which neural cortical areas exhibited activation that positively correlated with Urge score rather than other confounding factors. Therefore, exclusive masks involved in other confounding factors (i.e. Familiarity, Difficulty and Rhythm) were used to examine Urge-specific areas (non-overlapping areas). The statistical threshold of exclusive masks was set at $P < 0.001$, and was intended to reveal regions where one contrast did not overlap with those from one or more different contrasts.

In addition to identifying areas that positively correlated with Urge, the neural networks underlying Urge and imitation performance were also assessed using PPI (Friston et al., 1997). This study identified aspects of the right supplementary motor area (SMA) and bilateral midcingulate cortex (MCC) that were specific to Urge under the imitation condition. The SMA was expected to have a strong connection with mirror areas (e.g. pre-motor cortices and parietal cortices), and thus, a PPI regressor

was created (SMA \times Imitation-Observation) to determine which regions were more highly correlated with the SMA under the imitation condition than under the observation condition. A peak voxel of the right SMA cluster (8, -14, 66) identified by correlation analysis with Urge as a seed voxel was used to accomplish this. The statistical threshold was set at $P < 0.001$ and corrected to $P < 0.05$ for multiple comparisons using cluster size.

Post hoc analyses

To confirm that neural correlates of Urge were not due to some specific kinematic characteristics of the action, multiple regression analyses were conducted. Because there were four kinematic factors (Speed, Key motion, Motion type and Symmetry), and the individual action contained a combination of these kinematic factors, multiple regression analyses were conducted separately. Each of the four kinematic factors possessed various sub-categorical levels: Speed had two levels, Key motion had nine levels, Motion type had three levels and Symmetry had four levels. In the four multiple regression models for the four kinematic characteristics of the individual action, Urge was orthogonalized against the other levels, allowing identification of the remaining effect in the models, which was designated the Urge-specific effect. Moreover, in a similar manner, additional multiple regression analyses were conducted to provide further confirmation on the Urge-specific areas and reject the effects of explicit reasons (Difficulty, Rhythm, Familiarity and Urge). Urge was also orthogonalized against other parameters. The statistical threshold was set at $P < 0.005$ and the voxel size at $k > 10$ due to concerns about type II errors (i.e. missing true effects; Lieberman and Cunningham, 2009).

Results

Behavioral data

In the fMRI experiment, Urge showed significant correlations with Familiarity and Rhythm (Urge and Familiarity, correlation coefficient = -0.20 to $+0.94$, median = 0.40 , $t[36] = 6.89$, $P < 0.001$, two-tailed; Urge and Rhythm, correlation coefficient = -0.25 to $+0.83$, median = 0.32 , $t[36] = 7.40$, $P < 0.001$, two-tailed). No significant correlation was revealed, but there was a correlation trend between Urge and Difficulty (correlation coefficient = -0.69 to $+0.60$, median = -0.15 , $t[36] = -1.93$, $P = 0.061$, two-tailed).

fMRI data

Neural correlates of Urge. Significant positive correlations between Urge scores and neural activation were observed in the

right SMA and bilateral MCC under the imitation condition (Table 1 and Figures 3 and 4), but no significant correlations were observed under the observation condition. Although some overlapping areas were observed between Urge and Familiarity, there were no overlapping areas between Urge and Rhythm or between Urge and Difficulty. Parts of the right SMA and bilateral MCC were specific for Urge, but were not involved in Familiarity (right SMA: $t = 4.80$, $P < 0.001$; right MCC: $t = 4.54$, $P < 0.001$; left MCC: $t = 4.43$, $P < 0.001$; Table 1 and Figure 5).

Functional connectivity between Urge and imitation performance. PPI analysis revealed that the SMA exhibited greater functional connectivity with the bilateral occipital lobes, including the extrastriate body area (EBA), cerebellum, premotor area (PM), thalamus, putamen, inferior parietal lobule (IPL) and right superior temporal sulcus (STS) under the imitation condition relative to the observation condition (Table 2 and Figure 6).

Neural correlates of Familiarity, Difficulty and Rhythm. Significant positive correlations of neural activation with Urge, Familiarity, Difficulty and Rhythm scores are summarized in Table 3 and Figure 4. For the Familiarity score, there were significant positive correlations among the left angular gyrus (AG), left cuneus, medial prefrontal cortex (mPFC), bilateral superior frontal gyrus (SFG) and right post-central gyrus under the observation condition. Under the imitation condition, there were significant positive correlations among the mPFC, bilateral SFG, STS, MCC, left AG, left post-central gyrus, left precuneus, right cuneus and right cerebellum. For the Difficulty score, there were significant positive correlations among the bilateral IPL, inferior temporal gyrus, SMA, precentral gyrus, right ACC, right AG and right inferior frontal gyrus (IFG) under the observation condition. Under the imitation condition, there were significant positive correlations among the bilateral SMA, middle frontal gyrus and STS. For the Rhythm score, there were significant positive correlations between the right cerebellum and right lingual gyrus under the observation condition. Under the imitation condition, there were significant positive correlations between the bilateral cerebellum and left STS.

Post hoc analysis

To further examine Urge-specific brain regions, multiple regression analyses were conducted using the kinematic

characteristics of the actions (Speed, Key motion, Motion type and Symmetry). In all cases, the Urge-specific areas were replicated under the imitation condition (Supplementary Figure S1).

Discussion

The present findings demonstrate positive correlations between activation of the right SMA and bilateral MCC with the strength of a subjects' self-evaluated urge to imitate meaningless hand actions. Activation in these areas could not be explained by explicit reasons for imitation or kinematic characteristics of the actions. Furthermore, PPI analyses revealed functional connectivity between the SMA and brain regions associated with imitation performance. Therefore, the present results suggest that activated regions are crucially involved in the imitation drive of unfamiliar meaningless actions and exhibit functional connectivity with the actual imitation performance.

Neural correlates of spontaneously driven imitation

Several neuropsychological studies have shown that the SMA plays an important role in voluntary action (Okano and Tanji, 1987; Passingham et al., 1987; Mushiaki et al., 1991). Lesions in the SMA cause mutism and reduce spontaneous motor activity (McNabb et al., 1988; Lang et al., 1991; Stephan et al., 1999). Furthermore, it has been suggested that the SMA contributes to the programming of motor subroutines and forms a queue of time-ordered motor commands prior to the execution of voluntary movements via the primary motor areas (Roland et al., 1980; Lang et al., 1990, 1991).

The role of the MCC during spontaneously driven imitation appears to be similar to that of the SMA, because both areas have a tendency to be co-activated during manual tasks (Koski and Paus, 2000). However, clear distinct anatomical differences appear to exist between the SMA and MCC, and it has also been suggested that certain important functional differences exist between these two areas (Picard and Strick, 2001). In this study, the MCC appeared to correspond with the caudal cingulate zone (CCZ), which is considered a homolog of the dorsal cingulate motor area and/or the ventral cingulate motor area in monkeys (Paus et al., 1993; Devinsky et al., 1995; Picard and Strick, 1996). Previous studies have demonstrated that the CCZ plays a role in response selection, executive function, self-initiated movement, urge for action and the adaptive control of voluntary actions (Shima et al., 1991; Picard and Strick, 1996, 2001; Fink et al.,

Table 1. Brain activations correlated with Urge

Structure		MNI coordinate			T value	Cluster size	P value
		x	y	z			
Positive correlations with Urge							
SMA	R	8	−14	66	4.80	427	<0.001
Middle cingulate cortex	L	−2	−14	50	4.66	*	*
Middle cingulate cortex	R	2	−10	56	4.54	*	*
Urge-specific (excluding Familiarity)							
SMA	R	8	−14	66	4.80	232	0.008
Middle cingulate cortex	R	2	−10	56	4.54	*	*
Middle cingulate cortex	L	−4	−14	56	4.43	*	*

Coordinates (x, y, z), the t-value at peak activation, the Urge cluster size and the P value under the imitation condition are shown (voxel size: $2 \times 2 \times 2 \text{ mm}^3$; *the peak is in the same cluster as the other peaks). These coordinates were the results of positive correlations with Urge scores and Urge-specific scores (excluding Familiarity) regions. The level of significance was set at $P < 0.001$ and was corrected to $P < 0.05$ for multiple comparisons using cluster size. L: left; R: right.

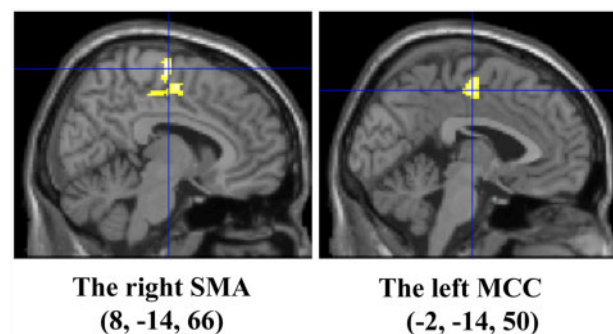


Fig. 3. Positive correlations between activation and Urge scores under the imitation conditions. Significant positive correlations between Urge scores and activation were observed in the right SMA and bilateral MCC under the imitation condition. No significant correlation was observed under the observation condition. The statistical threshold was $P < 0.001$, which was corrected to $P < 0.05$ for multiple comparisons using cluster size.

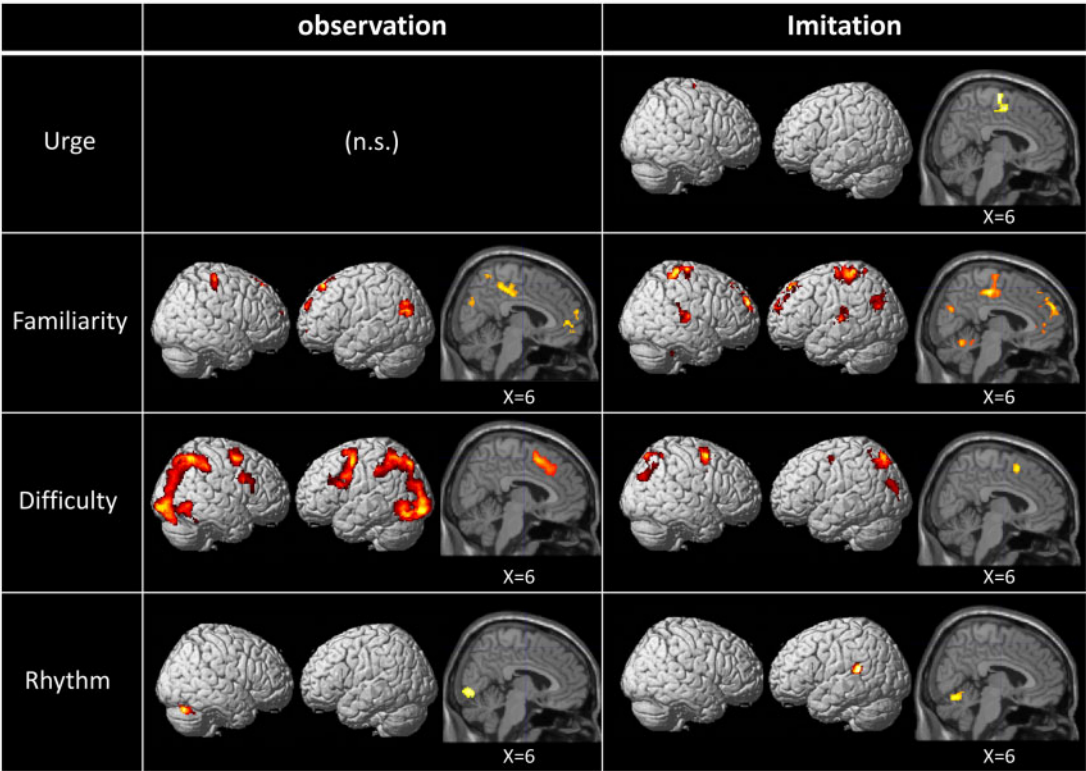


Fig. 4. Positive correlations between neural activation and the scores for each factor under the observation and imitation conditions. There were significant positive correlations of brain activation with Urge scores during the imitation condition, with Familiarity scores during the observation and imitation conditions, with Difficulty scores during the observation and imitation conditions and with Rhythm scores during the observation and imitation conditions. These figures are rendered on the right and left lateral surfaces and superimposed onto the parasagittal section ($x = 6$) of a standard brain using SPM8. The parasagittal sections are shown as parts of invisible images from the surface (see Table 2 for more details). The statistical threshold was $P < 0.001$ and was corrected to $P < 0.05$ for multiple comparisons using cluster size.

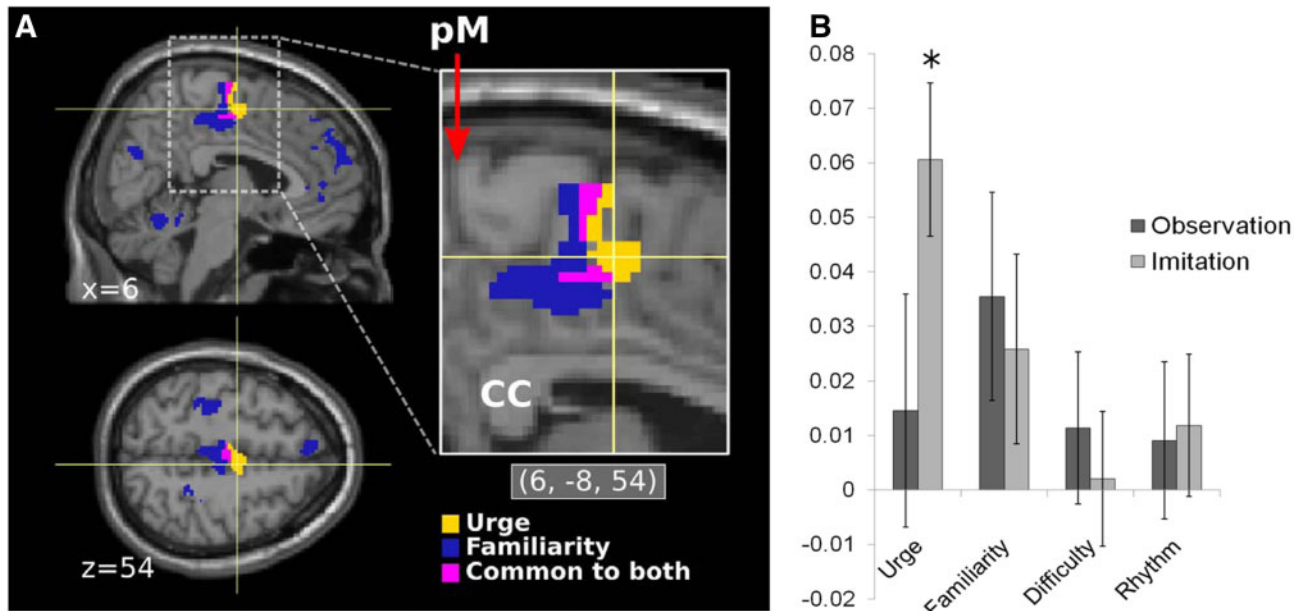


Fig. 5. Urge-specific correlations. (A) Brain regions showing significant positive correlations with Urge and Familiarity superimposed onto the parasagittal and horizontal sections ($x = 6$). Orange: Urge; Blue: Familiarity; Pink: Common to Both. (B) Activation profiles in the right MCC ($6, -8, 54$). The parameter estimates for Urge and the other scores under the observation and imitation conditions.

1997; Deiber et al., 1999; Debaere et al., 2004; Brázdil et al., 2006; Jackson et al., 2011; Shackman et al., 2011; Perini et al., 2013). Perini et al. (2013) investigated whether certain brain areas that

are consistently activated by pain in fMRI studies, such as medial premotor areas (including the cingulate motor area), reflect motor processing as it relates to voluntary action. They found

Table 2. Results of the PPI analysis

Structure		MNI coordinate			T value	Cluster size
		X	y	z		
Occipital lobe	R	16	−92	−10	7.49	9497
Occipital lobe	L	−46	−72	−4	6.33	*
Cerebellum	R	18	−88	−20	7.26	*
Cerebellum	L	−34	−80	−24	6.17	*
Inferior temporal gyrus	R	46	−72	−8	6.55	*
Inferior temporal gyrus	L	−46	−72	−8	6.33	*
Precentral gyrus	R	32	−8	56	6.97	5710
Inferior parietal lobule	R	48	−38	56	6.67	*
Superior temporal sulcus	R	56	−36	14	5.98	*
Precentral gyrus	L	−24	−12	52	6.02	5200
Inferior parietal lobule	L	−40	−54	56	6.27	*
Thalamus	R	18	−12	4	6.37	1438
Putaman	R	20	10	4	4.62	*
Thalamus	L	−16	−10	6	5.05	1108
Putaman	L	−24	−10	10	5.66	*

Coordinates (x, y, z), t-value at peak activation and size of the activated cluster (number of voxels; voxel size: $2 \times 2 \times 2 \text{ mm}^3$; * indicates that the peak is in the same cluster as other peaks). The level of significance was set at $P < 0.001$ and was corrected to $P < 0.05$ for multiple comparisons using cluster size. L: left; R: right.

that the CCZ did not respond to pain unless an action was performed, and that reaction times were faster during painful stimulation and correlated with CCZ activation. Thus, the authors proposed that the CCZ plays a vital role in the control and execution of context-sensitive behavioral responses during the experience of pain, or what can be considered the adaptive control of voluntary action. These observations may be associated with individual differences regarding the urge to imitate, which is supported by the individual differences observed in the urge to imitate ratings in this study, even though the participants watched the same stimulus. Therefore, parametric modulation was conducted to investigate the urge to imitate on a personal level in the first-level analysis. The findings indicated that this urge may play a role in the facilitation of actions as well as the adaptive control of actions.

Taken together, the present findings are consistent with those of previous studies that found that the SMA and CCZ are related to self-initiated movements, urge for action and adaptive control of voluntary actions.

Functional connectivity between Urge and imitation performance

As expected, PPI analysis performed in this study revealed that the SMA exhibited a strong correlation with frontoparietal cortical areas, such as the PM and IPL, under the imitation condition. This suggests that Urge is associated with imitation performance. Previous studies (Iacoboni et al., 1999; Buccino et al., 2004; Vogt et al., 2007) have reported that the frontoparietal cortical areas play a crucial role in imitation performance, as evidenced by investigations of the common coding paradigm, and indicate that the MNs have a strong relationship with imitation. Furthermore, Koski et al. (2003) suggested that the SMA is tightly coupled with MNs areas when subjects copy the actions of others. In this study, areas such as the EBA, cerebellum, right STS, thalamus and putamen appeared to be involved in this process. The EBA, cerebellum and STS are considered aspects

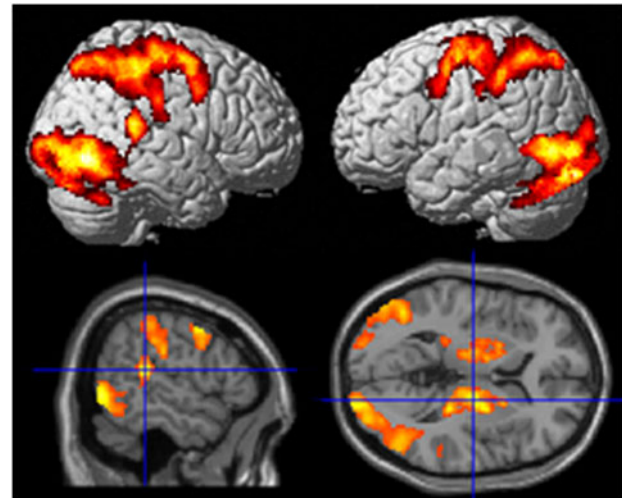


Fig. 6. Results of the PPI analysis. The SMA was expected to have a strong connection with mirror areas (e.g. the premotor cortices and parietal cortices), and thus a PPI regressor was created ($\text{SMA} \times \text{Imitation-Observation}$) to examine the regions that were more highly correlated with the SMA under the imitation condition compared with the observation condition. A peak voxel of the right SMA cluster (8, -14, 66) that was identified by a correlation analysis with Urge as a seed voxel was used to accomplish this. The statistical threshold was set to $P < 0.001$ and corrected to $P < 0.05$ for multiple comparisons using cluster size.

of MNs (Leslie et al., 2004; Iacoboni, 2005), while the thalamus and putamen contribute to motor control (Lehéricy et al., 2006). Therefore, the present results support the idea that the SMA represents Urge and is linked to actual imitation performance.

Lack of a significant correlation with Urge during the observation phase

In this study, we clarified the neural mechanism of imitation drive necessary for spontaneous imitation. However, a significant correlation with Urge was identified during the imitation phase but not during the observation phase. This lack of a significant correlation with Urge during the observation phase was unexpected because we assumed Urge would also occur during the observation phase. Therefore, we consider our finding to be indirect evidence of the neural substrate of spontaneous imitation. Meanwhile, we do not believe our findings reject the role of SMA or MCC.

Several reasons are possible as to why we could not find a significant correlation with Urge during the observation phase. First, this result could be explained by the exertion of inhibition on the imitation drive during the observation condition. In fact, the importance of inhibiting the urge to imitate in daily life has been emphasized repeatedly, because without inhibition, humans would imitate almost all the actions of others when observed (Brass and Heyes, 2005; Bien et al., 2009; Spengler, 2009). Based on the notion that imitation drive must be inhibited during observation, the reported inhibition system (Luna and Sweeney, 2004; Spengler et al., 2009; Wang et al., 2011; Cross et al., 2013; Hogeveen et al., 2015) was investigated using two types of analyses, including subtraction, in which the canonical models were contrasted (Observation condition - Imitation condition). Neural activation was observed in several areas, including the mPFC, anterior cingulate cortex, IFG and temporoparietal junction. The second analysis assessed the regions that negatively correlated with Urge during the

Table 3. Correlations of brain activation with each factor

Structure		MNI coordinate			T value	Cluster size
		x	y	z		
Familiarity						
Observation						
Angular gyrus	L	−56	−66	28	5.80	346
Superior frontal gyrus	L	−6	36	58	5.52	200
Medial prefrontal cortex	R	4	62	18	4.74	566
Cuneus	L	−2	−78	34	4.73	1195
Postcentral gyrus	R	40	−26	52	4.61	214
Imitation						
Medial prefrontal cortex	R	12	58	32	7.29	898
Superior frontal gyrus	L	−6	44	52	7.19	188
Middle cingulate cortex	L	−4	−28	44	7.19	1539
Angular gyrus	L	−52	−72	32	6.74	186
Postcentral gyrus	L	−32	−38	68	6.05	751
Precuneus	L	−2	−62	30	5.98	306
Cuneus	R	6	−72	26	4.80	*
Cerebellum (VI)	R	26	−50	−28	5.18	537
Superior temporal gyrus	L	−50	−22	8	4.84	434
Superior temporal gyrus	R	52	−20	10	5.22	171
Difficulty						
Observation						
Inferior parietal lobule	L	−34	−50	44	8.97	4824
Inferior temporal gyrus	L	−50	−66	−8	5.81	*
Inferior parietal lobule	R	28	−52	42	6.15	4796
Inferior temporal gyrus	R	54	−58	−4	5.23	*
SMA	R	8	10	52	7.07	1331
SMA	L	−2	20	44	5.71	*
Anterior cingulate cortex	R	12	24	30	5.57	*
Precentral gyrus	L	−30	−4	48	6.63	1268
Precentral gyrus	R	28	−6	50	6.59	670
Angular gyrus	R	28	−58	40	6.36	4796
Inferior frontal gyrus (triangular part)	R	58	24	26	4.91	296
Imitation						
SMA	L	−2	8	56	5.89	476
SMA	R	8	10	54	4.63	*
Middle frontal gyrus	R	38	2	62	5.63	547
Middle frontal gyrus	L	−28	−4	50	4.87	167
Superior parietal gyrus	L	−24	−72	46	5.15	768
Superior parietal gyrus	R	18	−74	58	4.53	461
Rhythm						
Observation						
Cerebellum (Crus I)	R	38	−68	−28	4.57	180
Lingual gyrus	R	4	−86	−4	4.16	288
Imitation						
Cerebellum (lobule IV/ V)	L	−4	−66	−12	5.58	538
Superior temporal gyrus	L	−52	−34	14	5.22	177

Brain activation was correlated with Familiarity, Difficulty and Rhythm under the observation and imitation conditions. Coordinates (x, y, z), t-value at peak activation and the size of activated clusters (number of voxels; voxel size: $2 \times 2 \times 2 \text{ mm}^3$; * indicates that the peak is in the same cluster as other peaks). The level of significance was set at $P < 0.001$ and was corrected to $P < 0.05$ for multiple comparisons using cluster size. L: left; R: right.

observation condition. In this case, the right SPL was activated. These results are consistent with findings from previous studies investigating the inhibition system (Durstun et al., 2002; Milham et al., 2002; Booth et al., 2003; Luna and Sweeney, 2004; Spengler et al., 2009; Wang et al., 2011; Cross et al., 2013; Hogeveen et al., 2015; see Supplementary Materials for more details).

We assumed that the latter reason for the lack of significance with Urge during the observation phase was associated with the stimuli used in this study. Imitation follows a hierarchical process and can, in principle, occur at various levels, such

as the action level (imitation of basic elements of behavior) or the program level (imitation of the organizational structure at any higher level of goal-directed behavior; Byrne and Russon, 1998; Lestou et al., 2008; Menz et al., 2009). Previous studies have suggested that goal-directed, meaningful and emotional actions have a greater impact on human brain activities (Rushworth et al., 2001b; Koski et al., 2002; Järveläinen et al., 2004; Castiello, 2005; Grosbras and Paus, 2006). However, this study focused more on the bottom-up cognitive processes and spontaneous status and, therefore, used meaningless actions and instructed

the participants to observe the actions passively. Thus, it was not surprising that a significant correlation was observed with the urge to imitate only during the imitation condition.

Neural correlates of Familiarity, Difficulty and Rhythm

This study primarily focused on imitation drive, but also evaluated brain regions related to other confounding factors such as Familiarity, Difficulty and Rhythm (see Supplementary Materials for further discussion).

In terms of Familiarity, extensive activities were observed in areas such as the left AG, left postcentral gyrus, mPFC, bilateral SFG and posterior cingulate cortex during both observation and imitation conditions. The activations under these two conditions were quite similar, and it appeared they shared action-related memory characteristics. Previous studies have revealed that these two areas are associated with episodic memories of familiar actions, people, objects and places (e.g. Calvo-Merino et al., 2005; Sugiura et al., 2005, 2009), consistent with the present results.

In terms of Difficulty, salient activation was observed in areas such as the bilateral IPL, EBA and bilateral ventral and dorsal PM during the observation condition. These results are consistent with studies on imitation learning (e.g. Buccino et al., 2004; Vogt et al., 2007), and suggest that human brains attempt to prepare motor patterns and motor sequences for action even if the action is difficult to perform.

In terms of Rhythm, the present findings support those of previous studies indicating that the cerebellum plays a crucial role in the coordination and control of motor activity (Thach et al., 1992; Strick et al., 2009, see also Kawato et al., 2011) and sensory auditory processing (Petacchi et al., 2005; Stoodley and Schmahmann, 2009; Baumann and Mattingley, 2010).

Association between Urge and Familiarity

Although this study attempted to dissociate the effects of urge to imitate from those of familiarity with an action or other explicit reasons for imitating an action by carefully preparing the stimuli used; however, it was not possible to separate these two factors completely. However, this suggests a close association between familiarity and urge to imitate, even for meaningless actions. Furthermore, it has been argued that experience may explain the better imitation performance of meaningful gestures than of meaningless gestures (Rumiati and Tessari, 2002; Vogt et al., 2007).

It has been proposed that imitation skill relies on sensorimotor associations acquired through the experience of observing the contingent actions of others in response to one's own actions; this is known as the associative sequence learning theory (Heyes, 2001; Heyes and Ray, 2004; Catmur et al., 2009). Similarly, ideomotor theory (Prinz, 1997; Stock and Stock, 2004; Shin et al., 2010) also explains why humans can imitate the actions of others (Brass and Heyes, 2005). These theories suggest that the internal representations of actions and the actions themselves are tightly linked, and that sensory feedback resulting from self-action is a crucial mediator of action control. The present findings support these theoretical frameworks and lead to the assumption that human brains are able to store sensorimotor-associated information. Based on these theoretical frameworks, it is possible that the present findings represent the individual imitation drive using this type of stored information.

Why infants imitate spontaneously

Although we cannot fully explain why infants imitate, we believe the results of this study provide an important step toward understanding the neural mechanism underlying spontaneous imitation. It is likely that SMA or CCZ dysfunction explains the lack of spontaneous imitation in children with ASDs and thus the failure of typical social skills and language development. Recent neuroimaging study reported abnormal activity in the CCZ or proximate region in autistic adults (Lombardo et al., 2010).

Limitations

This study has one primary limitation. The fMRI design did not include temporal jitters between conditions, and a correlation between the two task elements is possible. However, there was a 12.5-s rest and instruction period between the observation (10 s) and imitation (10 s) phases and, therefore, the predicted BOLD signals were expected to be significantly affected by each respective condition.

Conclusions

In summary, the present findings identify brain regions where an individual's urge to imitate was represented in the right SMA and bilateral MCC. These findings are consistent with those of previous studies, suggesting that these brain regions are related to self-initiated movement, urge for action and adaptive control of voluntary actions. In addition, the present findings confirm functional connectivity between the SMA and imitation performance areas using PPI, and indicate the right SMA triggers imitation performance. Furthermore, there was a close relationship between urge to imitate and familiarity of an action, which implies that the sensorimotor association or acquired motor skills obtained by an individual's experience may be stored in the brain to imitate actions when the need arises.

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Supplementary data

Supplementary data are available at SCAN online.

Conflict of interest. None declared.

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