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Neural Correlates of Rule-Based Perception and Production of Hand Gestures

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1. Introduction

Rule-based behavior is defined as flexible information processing that occurs across the sensory and motor domains. Recent studies on human and nonhuman primates have led to the identification of a set of brain regions that mediate flexible rule-guided behavior (White and Wise, 1999; Asaad et al., 2000; Hoshi et al., 2000; Wallis et al., 2001; Bunge et al., 2003; Sakai and Passingham, 2006, Bengtsson SL et al 2009). Hand gestures or postures have often been used as sensory signals and/or motor responses that are supposed to be produced under behavioral rules, each of which is unique to a behavioral context (Bunge, 2004). The number of possible hand gestures is virtually limitless, but a set of certain familiar hand gestures is often used in various cognitive contexts or under various behavioral rules. "Rock–paper–scissors" (RPS) is an example of a set of familiar hand gestures that has been used to make selections during games. The same hand postures in the RPS game are used for counting with fingers in a different context. On the other hand, observations of hand gestures or postures are known to activate the mirror neuron system, which include functions that are related to the imitation and/or understanding of actions (Iacoboni et al., 1999; Koski et al., 2002, 2003; Rizzolatti et al., 2004; Dinstein et al., 2007, 2008; Iacoboni and Dapretto, 2006; Iacoboni, 2009). When observers see a motor event that shares features with a similar motor event included in their motor repertoire, they are primed to repeat the same movement. Thus, given the natural tendency to imitate observed gestures, the brain regions involved in the observation and production of hand gestures guided by multiple rules has not been clear. To address this issue, we introduced a new rule-guided hand-gesture task that required subjects to produce an appropriate hand gesture in response to an observed hand posture according to two behavioral rules: the RPS-game rule and the number-based rule. Under these two different rules, the same hand gesture signified either rock–paper–

scissors or null–two–five. We hypothesized that performance of the hand-gesture task under guidance of multiple rules would require that the meanings of hand-gestures to be represented in a rule-specific manner and the supervisory or other control system must be recruited to balance the rule-guided behavioral systems with the mirror system to overcome a covert and automatic tendency to imitate observed hand postures.

2. Methods, results and discussion

2.1 Materials and methods

2.1.1 Subjects

Nineteen healthy right-handed male subjects (mean age: 22.2 years, age range: 22–28 years) volunteered to participate in this study. All subjects had normal vision, and none had a history of neurological or psychiatric illness. Written informed consent was obtained from each subject before their participation in this study. All procedures were conducted in accordance with the guidelines approved by The Office of Policy Coordination of the Tohoku University Graduate School of Medicine.

2.1.2 Rule-based hand-gesture task (Fig. 1)

The subjects wore a head-mounted display to view objects projected by a computer and pushed buttons embedded in a small box held in their right hands. Participants were asked to perform a task involving rule-based hand gestures, as described in detail in the following section. Before functional magnetic resonance imaging (fMRI) scanning, all participants were asked to perform a brief exercise as a pre-scanning task.

Subjects were asked to perform a task involving rule-based hand gestures (Fig. 1A). In each trial, participants were asked to gaze at a central fixation spot (white dot) that appeared on the screen for 1500–2500 ms. Next, one of three illustrations of hand shapes (rock, paper, or scissors) was presented on the screen as a sample stimulus for 500 ms (stimuli shown in Fig. 1B). After a delay of 2500–4500 ms, the subjects were asked to produce a hand gesture in response to instruction cues. Two rule conditions were used: the RPS-rule condition and the number-rule condition. Under the RPS-rule condition (rock beats scissors, scissors beats paper, paper beats rock), one of three instruction cues—"win," "draw," or "lose"—was presented to the subjects for 500 ms (Fig. 1B, right and middle rows). As shown in the example presented in Figure 1A, each subject was instructed to produce the scissors gesture after observing the paper stimulus in response to the instruction to win. Under the number-rule condition, rock represented null, scissors represented two, and paper represented five. The subject was asked to produce the hand gestures corresponding to the appropriate numbers according to three instruction cues: "more," "equal," or "less." For example, the subject was required to produce the scissors hand gesture (two) in response to the rock stimulus (null) when an instruction cue of "more" was given. Presented with a number depicted by simple hand gestures, the subjects were instructed to use hand gestures to indicate the next higher or next lower number. Under both conditions, the subjects were instructed to press a button after producing the hand gesture. The inter-trial interval was 3000 ms. All subjects practiced a short version of the task prior to scanning. The RPS-rule and number-rule conditions were blocked as shown in Figure1C.
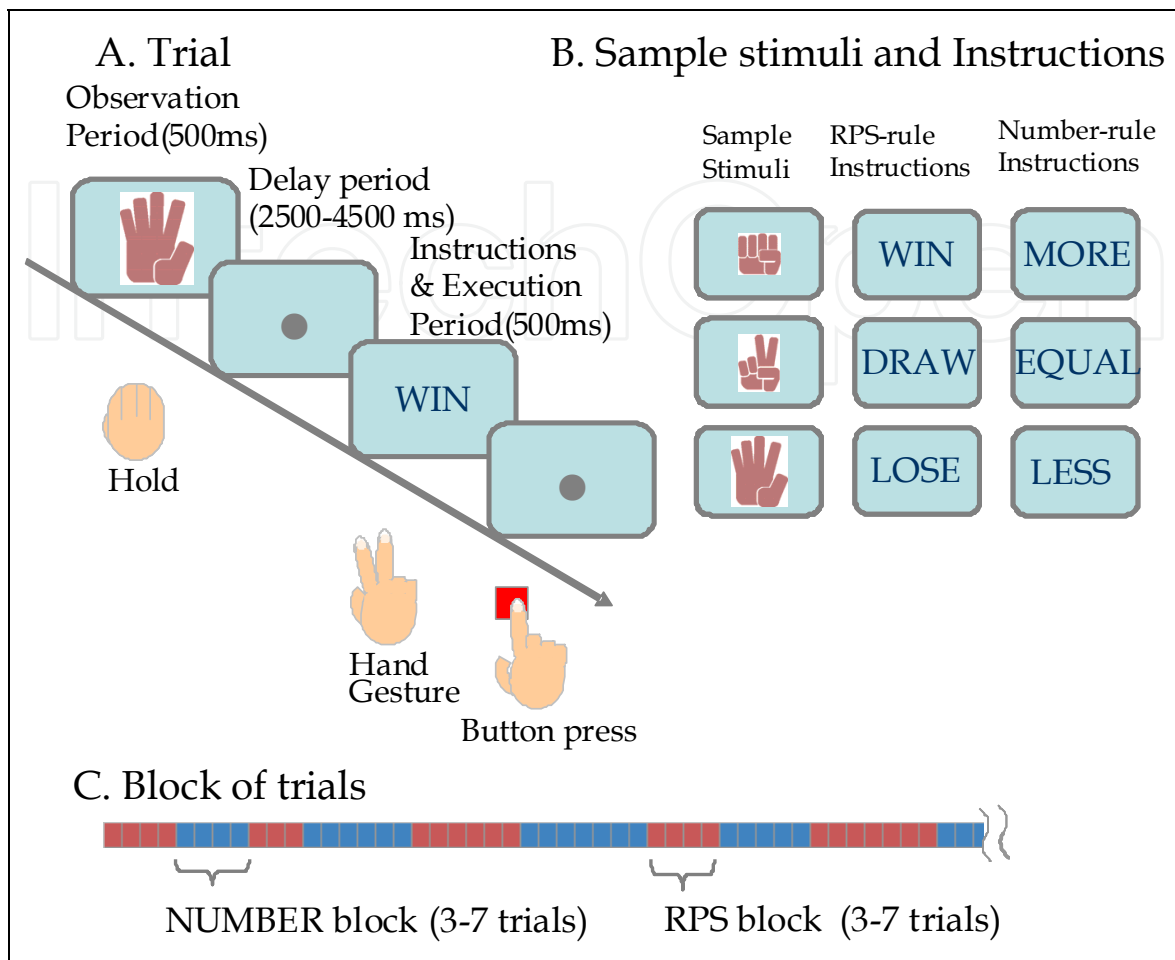
Fig. 1. Schematic diagram of Rule-based hand-gesture task. (A) Task sequence during fMRI scanning. During stimulus presentation, one of three illustrations of hand shapes was presented on a screen. During the instruction and execution periods, one of three instruction cues ("win," "lose," or "draw" under the Rock–Paper–Scissors-(RPS)-rule condition of the RPS block; or "more," "less," or "equal" under the number-rule condition of the number block) was presented on the screen. (B) Illustrations of hand shapes were used for sample stimuli and instruction cues used to guide the production of hand gestures. (C) A scanning session consisted of blocks of trials. Each block occurred under either the RPS- or number-rule condition and consisted of three to seven trials, yielding a total of 126 trials. The RPS block is represented in red and the number block is shown in blue.

2.1.3 MRI data acquisition

Images were obtained with a 3-Tesla MRI scanner (GE Signa Excite; GE Medical Systems, Milwaukee, WI, USA) equipped with echo-planar imaging capability. Functional MRI images were acquired using a gradient echo-planar sequence (repetition time = 3000 ms, echo time = 50 ms, field of view = 24 x 24 mm, matrix size = 64 x 64, flip angle = 90°, slice thickness = 7 mm (no interslice gap). We obtained 20 horizontal slices along the anteroposterior commissure AC-PC line, which encompassed the whole brain.

2.1.4 fMRI analysis

Image processing and statistical analyses of the fMRI data were performed using statistical parametric mapping (SPM5; Wellcome Department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk) and Matlab (MathWorks, Natick, MA, USA). The effect of head motion across the scans was corrected by realigning all scans according to the first one. A mean image created from the realigned echo-planar imaging (EPI) images was co-registered with the structural T1 image, and the structural images were normalized spatially to a standard template of $2 \times 2 \times 2$-mm³ voxel size in the space (Montreal Neurological Institute (MNI) space). The derived spatial transformation was applied to the realigned EPI images. Subsequently, the normalized EPI images were smoothed spatially with an 8-mm full-width at half-maximum Gaussian filter to reduce noise and minimize the effects of normalization errors.

The data for individual subjects were statistically analyzed using the general linear model in SPM5 software. The fMRI time-series data were modeled by a series of events convolved with a canonical hemodynamic response function. Global changes were adjusted by proportional scaling, and the low-frequency confounding effects were removed using an appropriate high-pass filter.

Statistical analysis was accomplished within SPM. The design matrix for blocked analysis was computed to characterize regionally specific effects under the RPS- and number-task conditions using a kernel that approximated the hemodynamic response function. We calculated contrast with a boxcar reference waveform using a t-value (SPM{t}) at each voxel. The SPM{t} was transformed to the unit normal distribution SPM{Z}.

To examine the activity changes related to each behavioral event during the task phase, we conducted an event-related analysis for each subject and a random-effect analysis for data from multiple subjects. In the single-subject-level analysis, we estimated the activity changes in response to the onset of sample stimuli under each rule condition. We also estimated activity changes in response to the instruction cues under each condition. According to these instructions, the subjects produced hand gestures that were identical to the sample when cued with "equal" or "draw." These conditions were considered to represent imitations of observed hand postures. As noted later in the Results section, the reaction times (RTs) for these two instruction cues were very brief and similar to each other, suggesting the operation of a priming effect related to observing a sample.

To identify rule-selective regions, we excluded regions affected by common priming effects based on the tendency toward imitation. In this sense, we considered activity changes in response to these instructions as baseline activity under the control condition. We then obtained the following two contrasts from each subject to identify rule-selective areas: the response to "win" or "lose" (RPS-rule condition) minus the response to "equal" or "draw" (control condition), and the response to "more" or "less" (number-rule condition) minus the response to "equal" or "draw" (control condition). Thereafter, we also identified rule-nonselective regions by performing a conjunction analysis of cortical activations common to number-rule and RPS-rule conditions.

We computed the group effect with a random-effect model using a one-sample t-test. Voxels were given a threshold of $p < 0.05$ using a maximal false-discovery rate (FDR), a method of

correcting for multiple comparisons. Additionally, we applied parametric modulation to investigate the region corresponding to performance (RT or trial frequency) using a between-block design. A voxel-level threshold of $p < 0.05$ (FDR) and an extent threshold of five voxels were reported in the parametric modulation. The MNI coordinates were nonlinearly converted into Talairach coordinates using the MNI2tal® conversion program (ftp://ftp.mrc-cbu.cam.ac.uk/pub/imaging/MNI2tal/mni2tal.m).

We used two types of software to identify anatomical and functional areas: the 'Talairach Daemon' client to identify Brodmann's areas (BAs) (http://ric.uthscsa.edu/ projects/ talairachdaemon.html) and the AAL plugin (http://www.cyceron.fr/web/aal anatomical_automatic_labeling.html) to identify functional activation maps.

2.1.5 Regions of interest (ROI) analysis

To quantitatively examine the context of the brain activities, we conducted an ROI analysis based on the statistical parametric map obtained by the event-related analysis. We hypothesized that activated brain regions were classified into rule-selective (number-rule or RPS-rule) areas for implementation of rule-dependent task sets and common areas for supervisory roles or active memory retrieval against the covert tendency to imitate observed hand postures. Under the number-rule condition, we selected first set of three areas [i.e., the superior parietal lobule (SPL), the intraparietal sulcus (IPS), and the premotor area (PMA)] in which number representations were found. Although subjects usually play RPS-games to win, subjects were asked to produce hand gestures even though a particular hand gesture resulted in a loss under our RPS condition. Thus, we selected second set of three areas [i.e., the orbitofrontal cortex (OFC), the anterior cingulated cortex (ACC), and the pre-supplementary area (pre-SMA)], which are involved in reward-based action selection or conflict resolution under the RPS-condition. We selected third set of three areas [i.e., the dorsolateral prefrontal cortex (DLPFC) for its role in executive functioning, the posterior cingulated cortex (PCC) for its role in the retrieval of memorized rules, and the supplementary motor area (SMA) for its role in memory-guided action selection] as nonselective areas common for both rules. We therefore defined the nine individual ROIs in each hemisphere of each subject.

The ROIs that reached a statistical threshold of $p < 0.05$ were presented as spheres centered on the peaks of clusters within a radius of 8 mm. The mean percentage of signal change (relative to a fixation period inserted between blocks) within each ROI was calculated for each subject and task using Mars Bar® (http://marsbar.sourceforge.net/).

2.2 Results

2.2.1 Behavioral data for the fMRI scanning task

To examine the effect of task condition on RTs, we plotted the averaged RTs and conducted statistical comparisons of the values obtained for these variables in response to each instruction cue (Fig. 2). Under the RPS-rule condition, the RTs in response to "draw" were significantly shorter than RTs in response to "win" [$t(339) = 4.21$, $p = 0$]. The RTs for "draw" were significantly shorter than RTs in response to "lose" [$t(351) = 7.11$, $p = 0$]. In contrast, under the number-rule condition, the RTs in response to "equal" were significantly shorter

than those for "more" [t(329) = 8.03, p = 0]. The RTs for "equal" were significantly shorter than those for "less" [t(335) = 11.35, p = 0]. Means and standard errors for all conditions are listed in Table 1. The shorter RTs for the "draw" and "equal" instructions under each rule condition may have reflected the rapid production of a hand gesture identical to the sample, reflecting the difference between the process of imitation and that of rule-based selection as well as the impact of the priming effect on the imitation of observed hand postures.
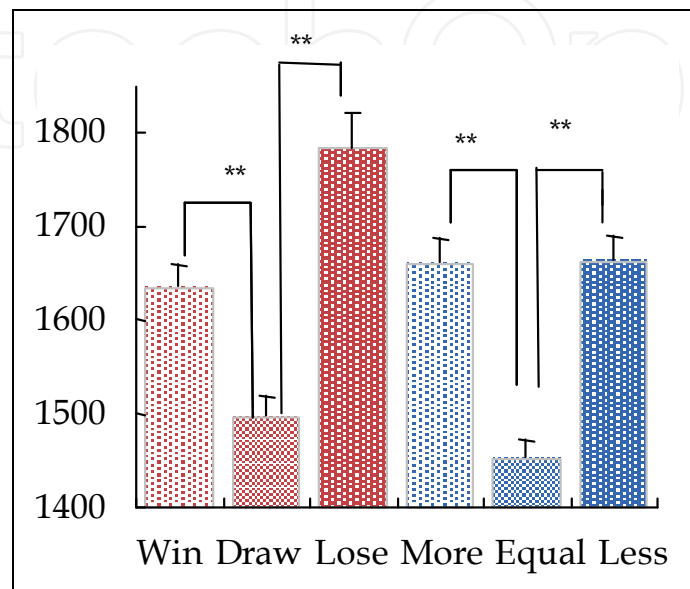
Fig. 2. Average response times of all subjects. (A) Plot of reaction times under six instruction conditions ("win," "draw," "lose," "more," "equal," and "less").

Instruction conditions	
RPS ruled	
Win	1634.67±23.43
Draw	1497.61±20.96
Lose	1784.8±38.35
Number ruled	
More	1661.36±24.43
Equal	1454.61±16.84
Less	1663.89±26.05
Values are means ±SE; msec.	

Table 1. The effect of instruction type on reaction time

2.2.2 Neural activity during the instruction and execution periods

We showed contrast activity changes in response to the instruction cues under the RPS-rule condition and the number-rule condition based on the event-related analysis explained in the Methods section. On the basis of these comparisons, instruction-related activity was

classified into three categories: RPS-rule-selective activity, which showed significantly greater changes in activity under the RPS than under the number condition [p < 0.05 (FDR)]; number-rule-selective activity, which showed significantly greater changes in activity under the RPS condition than under the number condition [p < 0.05 (FDR)]; and nonselective activity, which showed similar changes in activity under both the RPS and number conditions. (Fig.3).
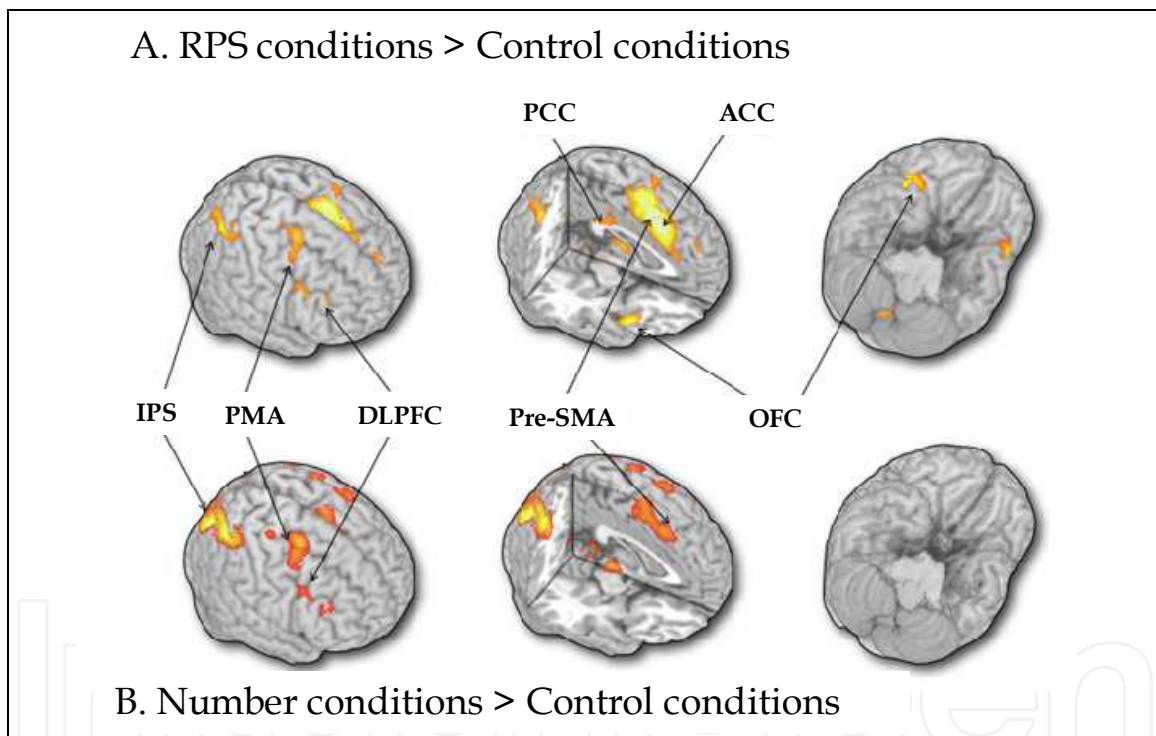

Fig. 3. Rule-selective activity during the execution period (A) Brain areas significantly activated in response to "win" or "lose" under the RPS-rule condition. (B) Brain areas significantly activated in response to "more" or "less" under the number-rule condition.

To quantitatively examine activation patterns, we performed a ROI-based analysis for the OFC, IPS, and DLPFC by extracting data on the mean percent signal changes at each ROI, as shown in 4A, 4B, and 4C, respectively. ROI analysis of rule-related activity during the execution period was listed in Table 2.
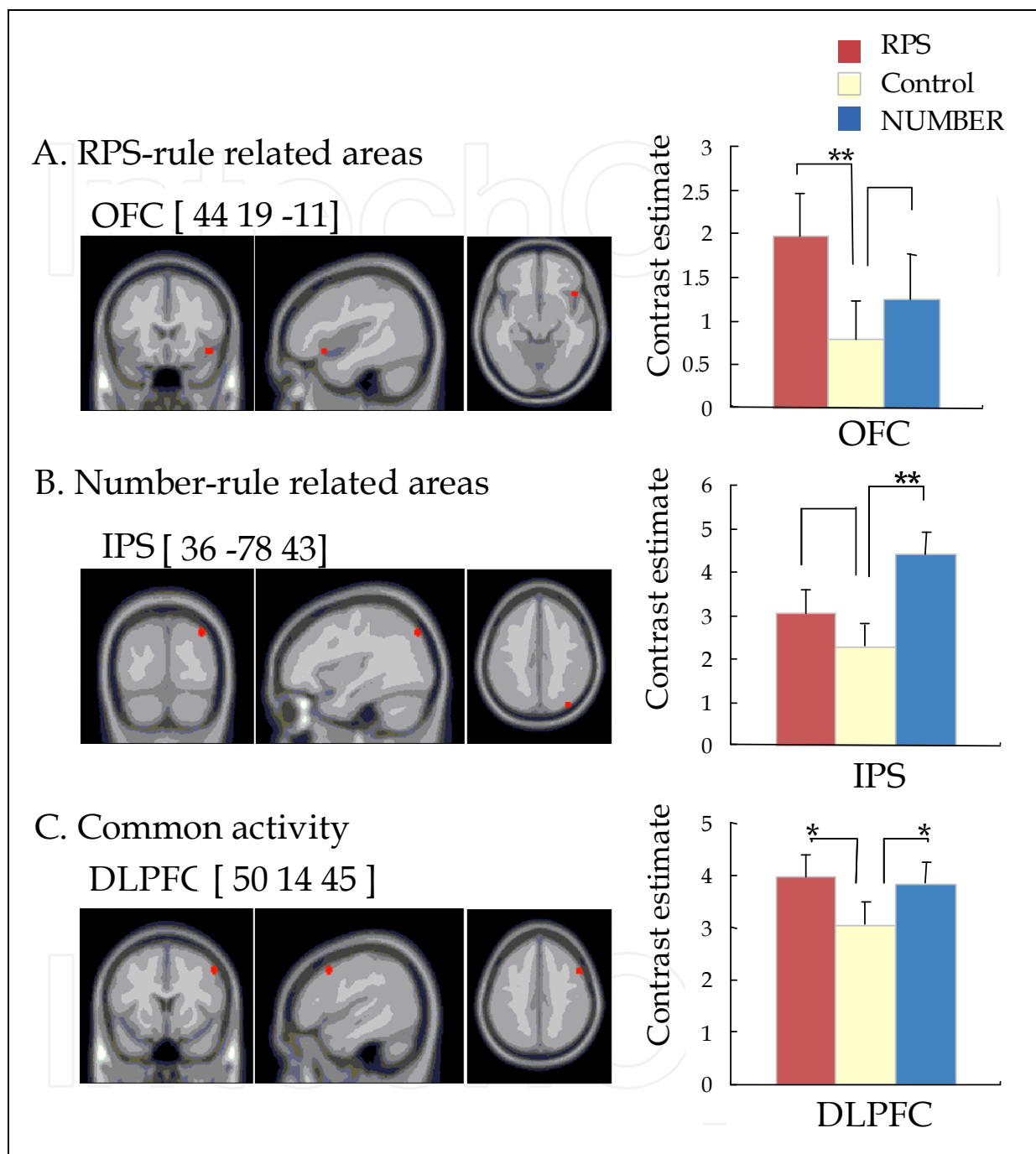
Fig. 4. Rule-related activity and ROI analysis. (A) The orbitofrontal cortex (OFC) was significantly more activated under the RPS-rule condition than under the control and number-rule conditions. (B) The intraparietal sulcus (IPS) was significantly more activated under the number-rule condition than under the control and RPS-rule conditions. (C) The dorsolateral prefrontal cortex (DLPFC) was significantly more activated under both the RPS- and number-rule conditions than under the control condition (Table 2).

Region of activation L/R Area			coordinates of peak activation			
			x	y	z	Z value
RSP > Number>ctrl						
ACC	L/R	24	4	-10	40	4.01
PreSMA	L/R	6	4	21	63	4.82
OFC	L/R	47	44	19	-11	4.51
Number >RPS> ctrl						
IPS	L/R	7/40	36	-78	43	4.22
PMA	L/R	6	-41	-2	62	3.71
SPL	L/R	40	-41	-54	60	3.96
Non-selective activity in RPS condition (Number > ctrl) and (RPS> ctrl)						
DLPFC	L/R	9	50	14	45	3.77
SMA	L/R	6	-4	-10	74	3.87
PCC	L/R	23	-4	-38	26	4.02
Non-selective activity in Number condition (Number > ctrl) and (RPS> ctrl)						
DLPFC	L/R	9	50	14	45	3.1
SMA	L/R	6	-4	-10	74	3.66
PCC	L/R	23	-4	-38	26	3.47

Table 2. ROI analysis of rule-related activity during the execution period

Furthermore, to quantitatively compare the rule-related activity in response to the "win" and "lose" instructions under the RPS-rule condition, we conducted a ROI analysis for the ACC (BA24) and OFC (BA47). We found that the "lose" and "win" cue elicited significantly greater changes in activity than the "draw" cue under the RPS condition (Fig. 5A). To quantitatively compare the instruction-related activity of the "more" and "less" cues under the number-rule condition, we also conducted a ROI analysis for the IPS (BA7/40) and the PMA (BA6). We found similar activity changes in response to "more" and "less" (Fig. 5B).
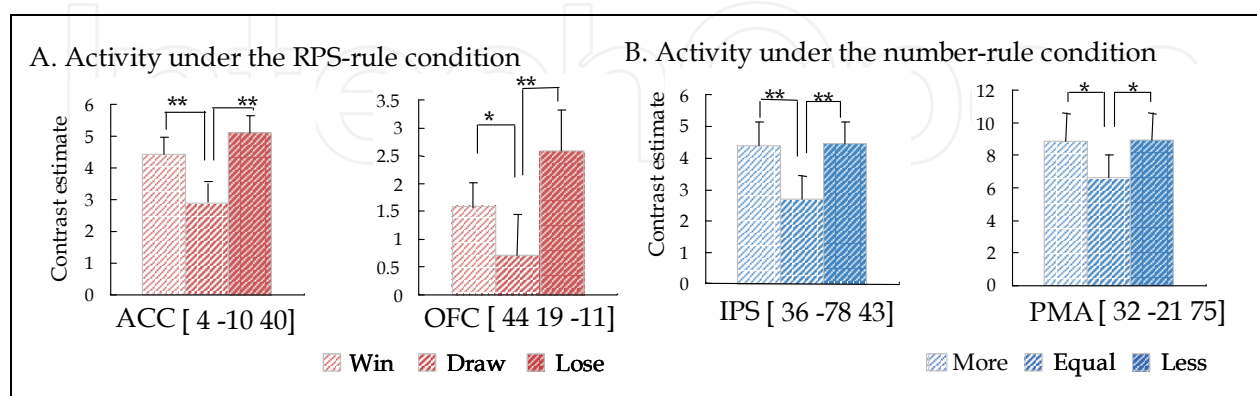

Fig. 5. ROI analysis of rule-related activity during the execution period. (A) The anterior cingulate cortex (ACC) and orbitofrontal cortex (OFC) were significantly more activated in response to "lose" and "win" than to "draw." (B) The intraparietal sulcus (IPS) and premotor area (PMA) showed similar activation in response to "more" and "less."

2.2.3 Neural activity during the observation periods

We examined brain activation during the observation period (Fig. 6) and in general found greater activation in various task-related areas under the number-rule condition than under the RPS-rule condition. Based on our findings of rule-selective activities in response to instructional cues and to sample hand shapes, we compared the rule selectivity for the two task periods. Areas showing number-rule selectivity during the instruction and execution periods were more active under the number-rule than under the RPS-rule condition during the observation period (Fig. 6B). However, areas showing RPS-rule selectivity during the instruction and execution periods were active under both conditions during the observation period (Fig. 6A). Several RPS-rule-selective brain areas were more active under the number-rule than under the RPS-rule condition.
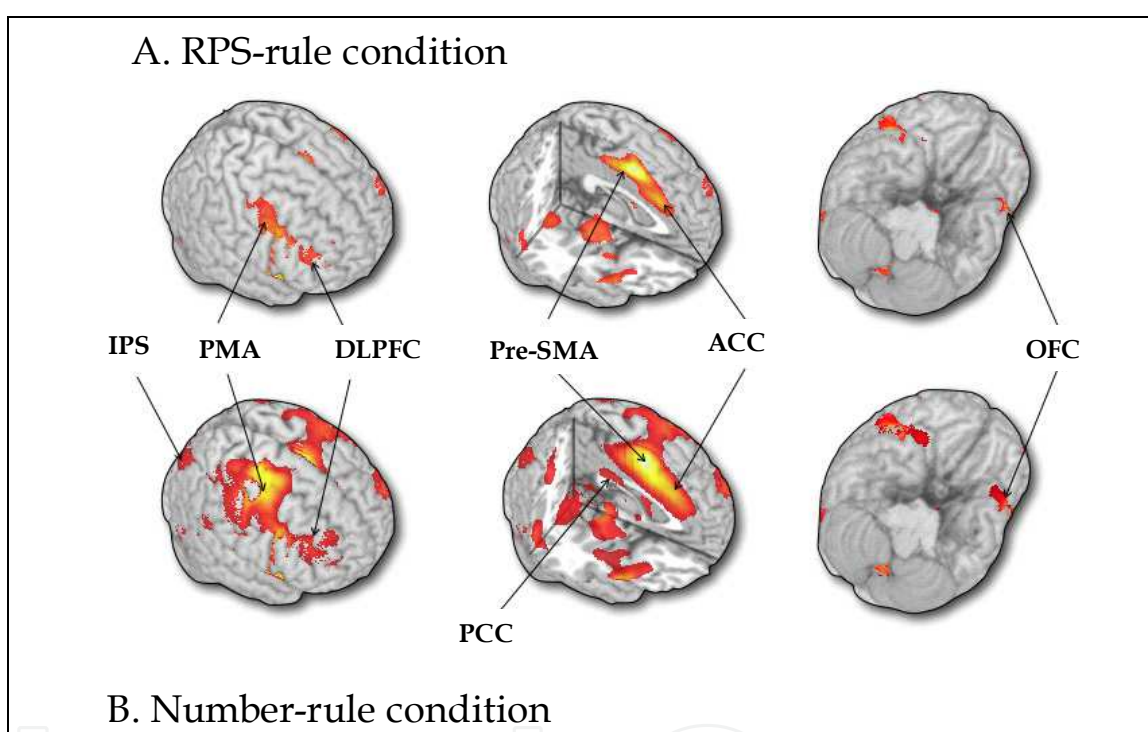

Fig. 6. ROI analysis of rule-related activity during the execution period. Brain areas activated in response to the hand-shape stimuli under the RPS-rule and number-rule conditions during the observation period. (A) Brain areas activated in response to the hand-shape stimuli under the RPS-rule condition. (B) Brain areas activated in response to the hand-shape stimuli under the number-rule condition.

To quantitatively examine changes in activity, we performed a ROI analysis on the IPS, PMA, ACC, and OFC. Both the IPS and PMA showed higher activation under the number-rule condition during the instruction, response, and observation periods (Fig. 7A). In contrast, the OFC was activated in response to the sample hand shape under both conditions. Unexpectedly, the ACC showed greater activation under the number-rule condition than under the RPS-rule condition even though this area was preferentially active under the RPS-rule condition during the instruction and execution periods and thus reflective of selective activity during the instruction and execution periods (Fig. 7B).
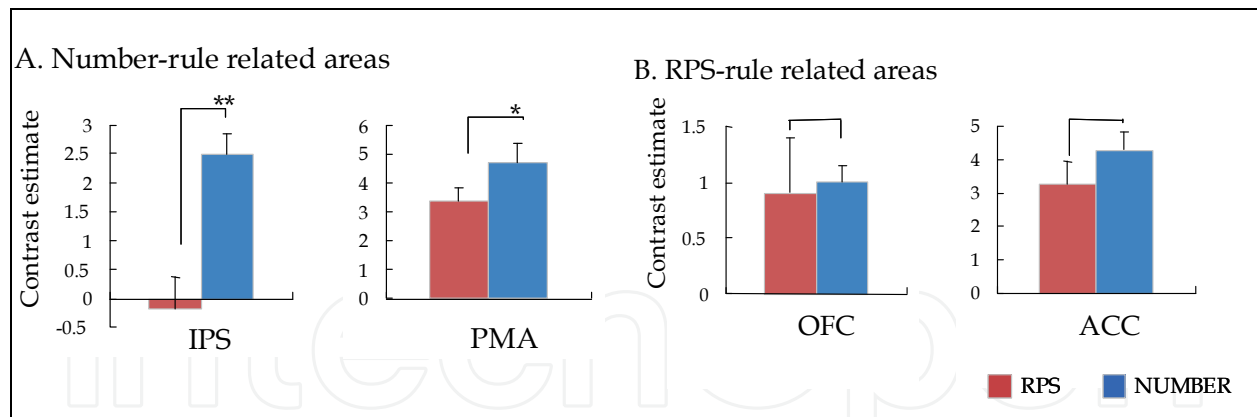
Fig. 7. ROI analysis of rule-related activity in the observation period. (A) IPS and PMA showed greater activation under the number-rule condition than under the RPS-rule condition during the observation and execution periods. (B) OFC and ACC showed greater activation under the number-rule condition than under the RPS-rule condition even though they are classified as RPS-selective areas.

2.3 Discussion

We defined the brain regions recruited for recognition and production using two behavioral rules. Rule one was based on the RPS game in which subjects were required to produce hand gestures in response to the observed sample hand postures according to one of three instructions: "win", "draw", or "lose" (RPS rule). The other rule two was based on number gestures in which subjects were required to produce number gestures by hand for the value of the observed hand posture in response to one of three instructions: "more", "equal", or "less" (number rule). A closed fist, extended index and middle fingers, and extensions of all fingers were gestures common to both rules, denoting rock, scissors, and paper, respectively, under the RPS-rule condition and null, two, and five, respectively, under the number-rule condition. We found that production of the same hand gestures recruited activation of different brain regions and that the IPS and the PMA exhibited distinct activation when subjects observed the sample hand shapes and produced the hand gestures according to the instructions under the number-rule condition. We also found that the ACC and the OFC exhibited distinct activation when the subjects produced the hand gestures under the RPS-rule condition. Under both "equal" and "draw" conditions, reaction times were shorter and rule-selective activities decreased compared to other conditions. These findings clearly demonstrated that observation of hand shapes evoked a priming effect for the mirror system Furthermore, both the ACC and OFC were active when the subjects observed the sample hand shapes, irrespective of the current rule condition. This finding indicated that observation of hand shapes also evoked covert activations in RPS rule-selective areas. The lateral prefrontal cortex (LPFC) was active under both rule conditions, suggesting a role coordinating the mirror and rule-guided gesture systems as a supervisory controller.

2.3.1 Mirror system, rule-based perception, and production of hand gestures

Rapid reproduction of the hand gestures representing equal in the number-rule and draw under the RPS-rule conditions suggested the priming effect of the mirror system. Observers

are primed to repeat a motor event that shares features with a similar motor event present in their motor repertoire upon encountering it. It means the greater the similarity between the observed event and the previous motor event, the stronger will be the priming effect (Prinz, 2002). Decreases in rule-selective activities also supported the covert effect of the mirror system.

A human mirror system has been elucidated by a substantial number of studies that focused on reactions to the observation of actions performed by others (Iacoboni et al., 1999; Koski et al., 2002, 2003; Rizzolatti et al., 2004; Dinstein et al., 2007, 2008; Iacoboni and Dapretto, 2006; Iacoboni, 2009). This mirror system forms a complex network consisting of an anterior area in the IFC that encompasses the posterior inferior frontal gyrus (IFG) and the adjacent ventral premotor cortex (PMC) as well as a posterior area in the rostral part of the inferior parietal lobule (IPL) (Iacoboni et al., 1999; Koski et al., 2002, 2003; Rizzolatti et al., 2004; Brass and Heyes, 2005; Dinstein et al., 2007, 2008; Iacoboni and Dapretto, 2006; Iacoboni, 2009). The rule-selective areas, such as the ACC and OFC, under the RPS-rule condition and the PMA (PMd) and IPS were not included in the conventional mirror neuron system (Gazzola V and Keysers C. 2009). One hypothesis about the functional role of mirror neurons is that mirror-neuron activity mediates imitation. Subjects in our study were required to observe hand shapes and execute hand gestures according to the two behavioral rules. In this task, subjects selected hand gestures that differed from the observed hand postures except in response to "equal" under the number-rule condition and "draw" under the RPS-rule condition. Indeed, our study identified rule-selective brain regions by noting areas characterized by significantly greater activations than those during the imitation of gestures following instructions of "draw" or "equal". We then calculated the contrasts in the activations associated with producing hand gestures that differed from those that were observed. Decreased activity in rule-selective brains regions suggested greater contributions of the mirror system for gestures following instructions of "draw" or "equal". Rule-guided system for arbitrary mapping sensory and motor events and the mirror neuron system for imitation based on direct sensory-motor mapping function competitively.

2.3.2 RPS-rule-related areas

We found that RPS-rule-selective activities in the ACC and OFC were involved in associating and integrating stimuli and rewards (Paus,2001;Schultz, 2004; Ridderinkhof et al 2004;Kringelbach, 2005; Coricelli et al., 2007; Rushworth et al., 2007; Wallis, 2007; Rolls and Grabenhorst, 2008; Seymour and McClure, 2008; Buelow and Suhr, 2009; Mainen and Kepecs, 2009). According to Wallis (2007), the OFC determines the potential reward outcome. Although a reward was not associated with any response or stimulus in our experiment, the subjects may have anticipated a potential reward because the RPS game is frequently related to rewards in daily life. Also, the ACC has been proposed to participate in conflict monitoring (Botvinick et al., 1999,2004; van Veen and Carter, 2005; Kerns, 2006). Under our RPS-rule condition, RTs in the "lose" situation were longer than those in the "win" situation. This asymmetrical distribution of RTs suggested that the subjects were biased toward selecting hand gestures associated with winning and wanted to do so even when the instruction was to lose. This tendency was associated with response conflict and

activated the ACC. Furthermore, a meta-analysis of neuroimaging data has suggested that the ACC and OFC were often co-activated when behavioral conflict was detected and behavioral change was required (Kringelbach, 2005).

This type of biased activation was not observed in comparisons of responses to the "less" and "more" cues. Indeed, the RTs under the "less" and "more" instructions did not statistically differ, and subjects did not show biases for either response. Based on this finding of biased responses, one can hypothesize that the instruction to lose frequently caused conflict because of a desire to win and led to a greater delay in the selection response than the instruction to win under the RPS-rule condition. The instructions to win or lose involved potential reward and/or conflict. In contrast, under the number-rule condition, more and less involved merely quantitative judgments about size and neutral decision-making about hand gestures.

Unexpectedly, RPS-selective areas such as the ACC and OFC, defined based on instruction-related activities, were covertly active under both the number and RPS conditions during the execution period. This pattern differed from that observed for the number-rule-selective areas, in which rule selectivity was maintained throughout the experiment. At least two possible interpretations for this pattern of activity can be proposed. One involves the implicit activation of RPS-related areas due to a stronger tendency to produce hand gestures in the RPS game than under the number-rule condition. Finger counting is often used in preschool education, but it is not used in the everyday lives of most adults. However, even adults use the RPS game. This difference in familiarity may cause the implicit activation of RPS-related areas even under the number-rule condition. Another possible interpretation concerns the behavioral conflict associated with the two behavioral rules. As mentioned in the previous section, the ACC and OFC were often co-activated in situations involving behavioral conflict. When hand shapes were presented to the subjects before the instructions, they may have experienced conflict between the two behavioral rules, one a relatively familiar RPS rule and the other a neutral number rule. According to both interpretations, observation of hand shapes elicited not only visual but also cognitive responses related to rule-based action selection.

2.3.3 Number-rule–related areas

Consistent with previous functional imaging studies showing that mental arithmetic activated the IPS bilaterally (Roland and Friberg, 1985; Dehaene et al., 1996, Piazza 2007), we found number-rule-selective activities in the IPS and PMC. Indeed, recent fMRI studies have revealed number-related parietal activation irrespective of the ways in which number stimuli were presented (e.g., sets or series of dots) (Piazza et al., 2004; Cantlon et al., 2006; Castelli et al., 2006; Piazza et al., 2006; Nieder and Dehaene, 2009). The PMC has also been reported to include number-related areas (Fridman et al., 2006; Kansaku et al., 2006, 2007). The number-rule-related areas were also active when the shape of the hand was presented as a sample stimulus under the number-rule condition. This anticipatory activation of number-related areas suggested that number-rule-selective areas were multimodal and related to perception and production of hand gestures when the rule mediating between stimulus and response was based on quantity.

2.3.4 Nonselective rule-related areas

We found that the LPFC was activated under both the RPS- and number-rule conditions. The LPFC has been implicated in rule retrieval in both nonhuman and human primates (Murray et al., 2000; Passingham et al., 2000). Human imaging studies have shown that the LPFC was active when individuals retrieved the meanings of rules and retained them over several seconds (Poldrack et al., 1999; Brass and von Cramon, 2002, 2004; Bunge et al., 2003). Thus, the LPFC is involved in rule retrieval and maintenance. Furthermore, the LPFC may be involved in suppressing the priming of the mirror system, which causes observers to reproduce observed hand postures. The LPFC is important to establish a cognitive set required for each rule condition (Sakai and Passingham,2006;Bengtsson et al 2009). It may also play an important role in rule switching and coordinating with the medial PFC including the pre-SMA (Rushworth et al., 2002; Wallis, 2007).

2.3.5 Limitations of present study and approaches to resolve difficulties

One of limitations of present study was that we did not able to show the results of functional connectivity among regions of interests. Main reason was because the number of subjects was not sufficient to draw firm conclusions. According to the previous study by Sakai K and Passingham RE.2006, activity of the LPFC reflected the process of implementing the rule for subsequent cognitive performance and showed rule-selective interactions with areas involved in execution of the specific rule-guided behavior. In our task, the LPFC may be involved in not just implmenting each behavioral rule, but also in controling production process of hand gestures primed by the mirror system but guided by multiple behavioral rules. For aapproaches to resolve difficulties about evaluation of multiple interactions among task related areas, we should collect more data and examine interactions between the mirror system and rule-guided system by using dynamic causal modeling which enables us to infer the causal architecture of task-related areas as coupled or distributed dynamical systems.

3. Conclusion

3.1 Major findings

To examine the brain areas involved in flexible rule-based perception and the hand gestures produced according to our covert tendency to imitate observed hand postures, we measured brain activation using functional magnetic resonance imaging while participants performed hand gestures based on the multiple behavioral rules of Rock–Paper–Scissors (RPS). Using this familiar practice, which involves multiple uses of the same set of hand gestures, subjects were asked to produce one of three hand gestures—rock (null), paper (five), or scissors (two)—in response to a sample hand shape and according to the instructions "win," "draw," or "lose" under the RPS-rule condition and according to the instructions "more," "equal," or "less" under the number-rule condition.

We found that the intraparietal sulcus (IPS) and the premotor area (PMA) exhibited distinct activation when the subjects observed the sample hand shapes and produced the hand gestures according to the instructions under the number-rule condition. We also found that the anterior cingulate cortex (ACC) and the orbitofrontal cortex (OFC) exhibited distinct

activation when the subjects produced hand gestures under the RPS-rule condition. Under both the equal and draw conditions, reaction times were shorter and rule-selective activities decreased compared to those under other conditions, suggesting that the priming effect of the mirror system influenced rule-guided behaviors. Furthermore, both the ACC and OFC were active when the subjects observed the sample hand shapes, irrespective of the current rule condition. These findings demonstrated that the observation of hand shapes evoked a priming effect such as that demonstrated by a mirror system and elicited covert activations in rule-selective areas. The lateral prefrontal cortex was also recruited in coordinating the mirror and rule-guided gesture systems.

3.2 Implication and summary diagram

Figure 8 presents a diagrammatic depiction of our two hypothesized rule-guided systems, the mirror and the supervisory systems. According to this diagram, observation of hand postures initially evokes the priming effects of the mirror-system. Rule-guided behavior systems, with the help of top-down signals from the DLPFC, seem to override mirror-system priming in the imitation of observed hand gestures. In two rule-guided systems, observation of hand gestures preferentially activates the ACC and OFC, which are selective for RPS-rule behavior during the execution period but are activated under both conditions during the observation periods. Top-down signals from the DLPFC in involved in
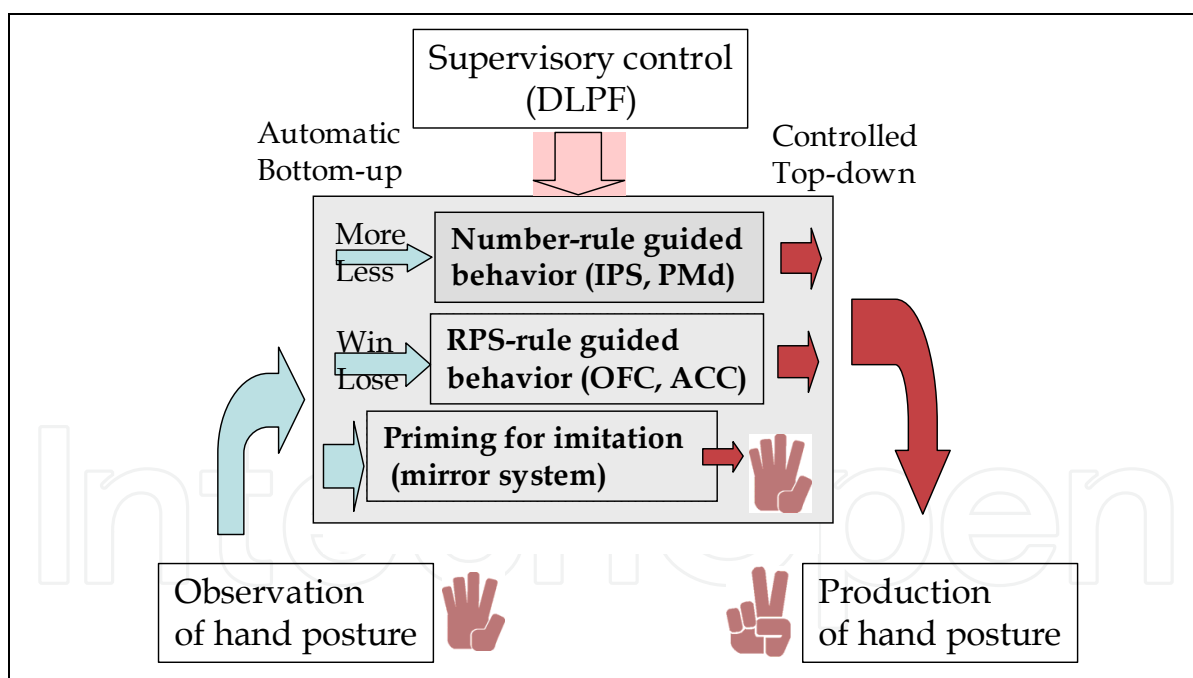

Fig. 8. Summary diagram. The number-rule guided behavior system, RPS-rule guided system, and mirror system function in parallel. Observation of the hand gesture automatically evokes the mirror system and preferred rule condition (RPS) in a bottom-up manner. When a rule-guided behavior is specified by instruction cues, a supervisory control signal adjusts the flow of information via top-down signalling. In the case depicted, some instructions specify the number-rule condition and others are guided by the number-rule system.

coordinating not only mirror system but also two rule-guided systems. During the execution periods, subjects are able to select appropriate hand gestures under the supervisory control of the DLPFC. In summary, observation of hand postures evoke automatic parallel activation of rule-related structures based on its preference in a bottom up manner, then appropriate hand gestures were produced based on the current status of the valid rule with the help of controlled top-down signal from the DLPFC.

3.3 New developments and future prospective

As we mentioned in introduction, the number of possible hand gestures is virtually limitless, but a set of certain familiar hand gestures is often used in various cognitive contexts or under various behavioral rules. In current studies, we examined brain regions related to observation and productions of simple hand gestures and postures without complicated spatiotemporal structures. However, hand gestures are often produced in space and in a sequential manner. Well-controlled studies using non-human primate have revealed many cortical motor areas, especially medial frontal motor areas, involved in control of sequential motor actions (Mushiake et al 1992; Hikosaka et al 1999;Shima K, Tanji J.2000;Tanji J.2001). Numerous functional imaging studies have found active foci in the cerebral cortex including the medial frontal cortex associated with the performance of a variety of sequential movements by human subjects (Shibasaki et al 1993; Deiber et al 1999;Kansaku et al 2006). The mirror system may contribute to imitation and understanding of complicated actions such as sequential movements performed by others (Rizzolatti et al., 2004; Iacoboni and Dapretto, 2006; Iacoboni, 2009). According to our current study, the dorsal premotor areas may contribute to rule-guided behaviours. A question arise which areas are involved in observation and production of rule based sequential hand gestures. Furthermore on the basis of fundamental properties of mirror neurons, Rizzolatti and Arbib (1998) proposed a hypothesis that the mirror neuron system represents the neurophysiological mechanism from which language evolved. But there are still explanatory gap between gestures and language based on the mirror neuron system (Hickock 2010). To narrow this explanatory gap, brain mechanisms underlying a sign language may provide important information about this issue (Poizner et al 1990), because the sing language is the visual-gestural language and a fully developed natural language with highly complex grammatical rules. Complex expressions through sign language include the recursive application of hierarchically organized rules. Further studies of rule based hand gesturers will provide more comprehensive view of neural mechanisms underlying observation and production of action for communication.

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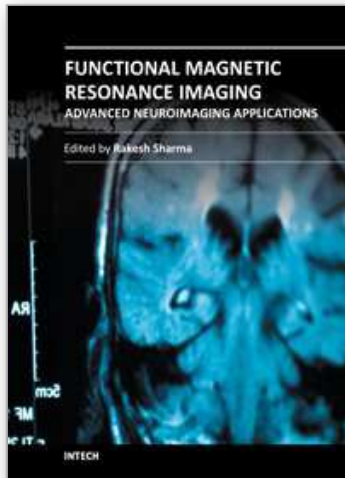
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