An imaging study on human action selection using hierarchical rules

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Abstract

To adapt to a dynamic environment, appropriate behavioral switching is necessary. In most real-world problems there are numerous possible actions, and it is often impossible to select the optimal action by evaluating all of them. Even in such a situation, humans can select an action efficiently by searching only a subspace of the whole action space. In this study, we design a Multi Feature Sorting Task in which the behavioral rules have a hierarchical structure, and conduct an fMRI experiment using the task. This task consists of two kinds of rule switches: a higher-order switch to search for a rule across different subspaces, and a lower-order switch to change a rule within the same subspace. The results of our imaging study show that the left inferior frontal gyrus is involved in the higher-order switch, and the right fronto-polar and right dorsolateral prefrontal cortex are significantly activated with the lower-order switch. We also suggest a functional model for the prefrontal cortex which explains the hierarchical rule-switching mechanism.

1 Introduction

In the real environment around us, there are numerous possible behaviors in each situation, and it may be impossible to immediately make an appropriate decision by evaluating all of them. To adapt to a dynamic environment, humans must seek action candidates efficiently and select the best one within a limited time. Recent studies in the engineering field suggest that a hierarchical structure of action candidates is useful for effective action selection [2][18], and an analogous method may be performed in human behavioral decisions. For instance, when we search for a lost article in the house, we will first check the most likely places rather than search the house uniformly. Such a searching scheme uses a hierarchical structure of available information; the whole search space is divided into subspaces, and a local optimization problem in one subspace is first solved. This hierarchical approach is effective as a computational algorithm and reasonable for a human behavioral model. However, it has been unclear how such a hierarchical mechanism operates in the real brain.

Assuming a human selects an action according to behavioral rules, he/she should switch between rules in response to environmental changes. The Wisconsin Card Sorting Task (WCST) [7] is one of the best-known tasks for studying such a rule-switching process. In WCST, the subject is required to discover a hidden correct rule from multiple possible rules using true/false feedback given correspondingly to the selected rule. Since the correct rule often changes without notice, the subject should try a new rule if he/she receives a false feedback. Many imaging and lesion studies have shown that prefrontal cortex is closely involved in solving WCST [1][6][9][12][19]. One study using a modified WCST with a variable number of rules revealed that the bilateral rostral inferior frontal sulcus (BA45/44) was activated when a subject switched rules due to environmental changes (correct rule changing) [9]. In contrast, another imaging study using a categorization task suggested that the bilateral fronto-polar prefrontal cortex (BA10) and left superior frontal sulcus (BA9/10) were related to rule switches [17]. Although both of these tasks needed rule-switch processes, different regions of the prefrontal cortex were reported as being engaged in rule-switch functions; however, functional segregation of these regions has yet to be clarified.

Existing studies based on rule-switching tasks assumed that possible rules were independent of each other and that a feedback for used rule had no clue about the new correct rule; thus, a subject should examine all rule candidates uniformly. Since we aim in this study at specifying the brain regions involved in a hierarchical rule searching mechanism, we have designed a Multi Feature Sorting Task in which the behavioral rules have a hierarchical structure. All rules in our task are categorized into two meta-rules, and hence there are two kinds of rule switches: a meta-rule switch (higher order switch) to search for a rule belonging to the other meta-rule class (subspace), and a rule switch (lower order switch) to change rules within the same meta-rule class subspace. Using this newly devised task, we conducted an fMRI experiment which showed that the different regions were activated during higher and lower order rule switching. This result suggests that different regions in the prefrontal cortex may cooperate to solve action selection problems in complicated situations.

2 Methods

2.1 Subjects

Eight healthy subjects (7 males and 1 female) participated in this experiment. Before scanning, all subjects were instructed about the aims and procedures of the experiment, and gave their written informed consent which was reviewed and approved by the ethical committee of Advanced Telecommunications Research Institute International (ATR). All subjects were graduate students with no history of neurological or psychiatric disorders. Each subject was paid a fixed monetary reward regardless of task performance. To acquire proficiency in the task, all subjects practiced a training task equivalent to the scanning one until they achieved a prescribed score on the day before scanning.

2.2 Multi Feature Sorting Task

In this study, we designed a Multi Feature Sorting Task in which the subject was required to sort three figures with multiple features using a rule (Fig.1). The three figures were displayed on a screen in the MRI device, and the subject sorted them by pushing the corresponding three bottoms one by one. At the center and the top of the screen, a fixation cross and a trial bar were displayed, respectively. There were three features: “number of vertices”, “size” and “brightness”, and each figure was categorized as “large”, “middle” or “small” for each of these features. For example, a large dark square would be represented as “number of vertices: middle; size: large; brightness: small”. The features of each figure did not overlap with other figures displayed simultaneously. Since a set of three figures can be sorted in two ways, “ascending order” and “descending order”, there are six sorting options in total. For example, “descending order for the number of vertices” corresponds to the sorting order pentagon, square, and triangle. Subjects performed such sorting twice using the same or different rules within a single trial (Fig.1(a)). Namely, after the subject sorted three figures (stimulus 1) by pushing three buttons, the next three figures (stimulus 2) were displayed to sort once again. This defined the subject’s behavior within one trial. The fixation cross was red for 2 sec after appearance of a stimulus, to encourage a response, and was yellow thereafter. Subjects were instructed to sort three figures by pushing buttons three times during the red fixation period; if the subject could not complete a sorting task within the red fixation period for the first and/or second stimuli in a trial, it was regarded as a mis-trial. To make a hierarchical structure for the sorting rules, a favorable set of two sorting behaviors was integrated into six rules, and these six rules were categorized into two meta-rules (Table 1). One meta-rule was a “feature rule” which focuses only on the combination of features (“number of vertices”, “size” or “brightness”) in a set of two sorting behaviors and not on sorting order (“ascending” or “descending”). The other was an “order rule” which focuses only on permutations in the two sorting behaviors regardless of the features used in sorting.

Table 1. Six rules and two meta-rules

“Feature rule”
- The first sorting is “number of vertices” and the second sorting is “size”, or vice versa
- The first sorting is “number of vertices” and the second sorting is “brightness”, or vice versa
- The first sorting is “size ” and the second sorting is “brightness”, or vice versa

“Order rule”
- The first sorting is “ascending order” and the second sorting is “descending order”
- The first sorting is “descending order” and the second sorting is “ascending order”
- The first and second sorting orders are the same as each other

For each trial, there is a hidden ‘correct’ rule selected from the six rules in Table 1, and the objective for the subject is to perform a pair of sorting behaviors according to the correct rule. However, the sorting rule determined by

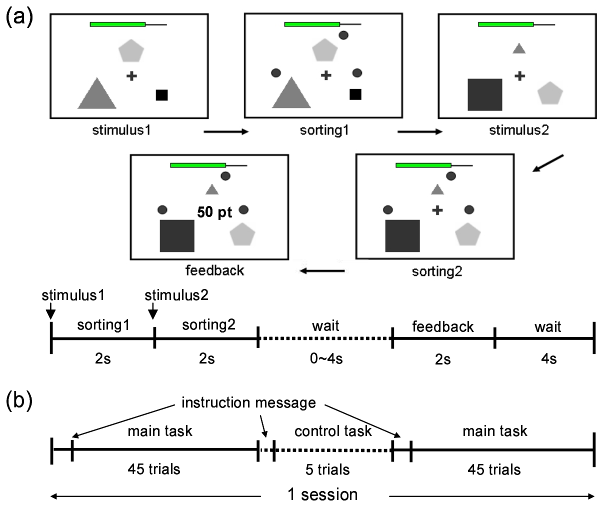

Figure 1. Multi Feature Sorting Task. (a) Stimulus and time design of a single trial. (b) Design of a single session.

the subject may not be the correct one. After the subject finished a trial, feedback was displayed according to the used sorting rule and the correct rule. For this task, we designed a probabilistic feedback. When the used rule agreed with the correct rule, the subject was given 50 points with 90% probability but 0 points with 10% probability. When the used rule was different from the correct rule, the subject was given 0 points with 90% probability but 50 points with 10% probability. Feedback was displayed in the center of the screen. To maintain the subject's sensitivity to a feedback signal, it was displayed at a variable time interval of $0-4$ sec after the trial completion. If the trial was a miss, the subject was given a caution message but no point feedback. All subjects were informed that the feedback was to be given in a probabilistic manner, but the rate of probability was not revealed. When the rule used agreed with the correct rule in any three among five successive trials, the correct rule was changed to another one without notification to the subject. Otherwise, the correct rule was the same as that in the previous trial. When the correct rule was changed, the new rule was selected with a higher probability (about 70%) from the same meta-rule class than from the other meta-rule class; subjects were told that this would be the case. Accordingly, the subject was required to perform "exploration", i.e., searching for a new rule, or "exploitation", i.e., continuing with the same rule as the previous one, based on the outcome of previous tasks. Because the outcome is probabilistic, this decision is an introspective one. There were thus two kinds of "exploration" actions, "a rule switch within the same meta-rule" and "a rule switch accompanied by a meta-rule switch". Further details are given in section 2.4. Note that there was no chance that a rule used by a subject matched two or more of the six correct rules.

A control task was conducted to determine the baseline of imaging analysis. In the control task, the basic experimental procedure, consisting of stimuli and the requirement for subject's behaviors, was the same as the main sorting task, while the fixed correct rule for all trials was given as a visual message at the beginning of the control task. Thus, subjects did not need to select a rule themselves. One session consisted of the first main task (45 trials), a control task (5 trials) and the second main task (45 trials), and each subject performed 3 sessions in the experiment (Fig.1(b)). Before scanning, subjects were instructed to push the sorting buttons under their right hand accurately and quickly.

2.3 Scanning Procedures

Using a whole-brain 1.5-tesla scanner (Magnetic Eclipse; Shimadzu-Marconi, Kyoto, Japan), functional images were obtained with T2*-weighted echo planner imaging (EPI), with blood oxygen-level depletion (BOLD) contrast. The volumes were acquired continuously every 2.0 sec (TR) with 20 slices of 5 mm thickness (TE: 48 msec, FA: $80°$, FOV: 192 mm, matrix size: 64×64). The first six (12 sec) EPI images in each session were excluded from the analysis to avoid the effect of T1 equilibrium. During one session, 560 EPI images were acquired. To investigate anatomical localization, T1-weighted three-dimensional images were acquired (TR: 12 msec, TE: 4.5 sec, FA: $20°$, FOV: 256 mm, matrix size: 256×256, thickness: 1 mm, 191 slices).

2.4 Imaging Analysis

Imaging data were analyzed using Statistical Parametric Mapping 99 (SPM99; Wellcome Department of Cognitive Neurology, London, UK). All functional images from each subject were realigned with the first image, using rigid transformation, and then the slice timing was corrected. After that, EPIs were registered to the individual anatomical image. The EPI images were normalized using parameters such that anatomical T1 images were normalized to the MNI (Montreal Neurological Institute) template. The normalized EPIs were spatially smoothed with a Gaussian kernel of 10 mm (FWHM).

We excluded imaging data for mis-trials. We then defined an event-block as 10 sec, such that the onset was the feedback of the previous trial and the end was the finish time of the second sorting in the current trial. For the analysis, three kinds of events-blocks were extracted from all event-blocks according to the subject's behaviors in the corresponding trial. The first was "meta-rule switch (MSW)",

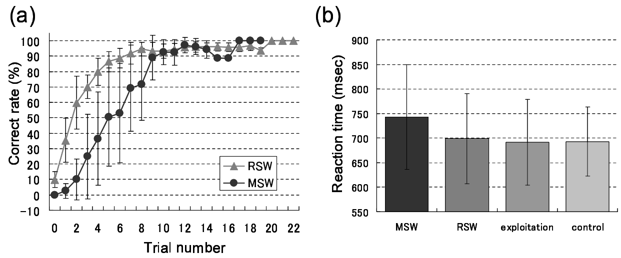

Figure 2. Behavioral analysis. (a) Time course of the correct rate after each of the two kinds of rule changes. (b) Reaction times for the four event conditions.

in which a subject tried a new sorting rule whose meta-rule class was different from the previous one. The second was "rule switch (RSW)", in which a subject used a different rule within the same meta-rule class as the previous one. Note that the difference between rule and meta-rule switches could be distinguished based only on the subject's behaviors. The third was "exploitation", in which a subject used the same rule as in the previous trial, and the rule was the correct one. Event-blocks not categorized in any of these three kinds were excluded from the analysis. The MSW and RSW were the same in terms of selecting one rule out of the six possible rules, but differed in that the MSW required a switch process between two meta-rules. The "exploitation" differed from MSW and RSW because no rule switches were necessary. All event-blocks were convolved with a homodynamic response function (HRF), and the control task was designed as an epoch which defined base activation. Six realignment parameters were also designed as regressors to eliminate moving artifacts. The data were high-pass-filtered using a low-frequency cosine function with a cut-off time of 60 sec. To account for inter-subject variability and to allow statistical inference at the population level, one sample *t*-test for statistical significance of group random effects was used. For comparison between MSW and RSW, the threshold at the voxel level was set to $p<0.01$ (uncorrected), and for that between RSW and "exploitation", it was set to $p<0.001$ (uncorrected). After that, cluster level analysis was applied with $p<0.05$ (corrected). We also conducted a time-course analysis of regions found to be significantly activated in the group analysis. The activation level for each region was represented as the average of signal intensities of all voxels within the region. These time course data were smoothed using a high-pass filter with a cut-off time of 100 sec and a low-pass filter with a cut-off time of 8 sec.

3 Results

3.1 Behavioral Results

To examine task performance, we applied a paired *t*-test to all behavioral data comprising three sessions each for all of the eight subjects.

In the Multi Feature Sorting Task, the correct sorting rule was changed depending on the subject's behavior, and there were two types of rule changes: a "meta-rule change" in which a new correct rule is selected from the other meta-rule class, and a "rule change" in which a new correct rule is selected from the current meta-rule class. The number of correct rule changes varied among subjects; the average number was 40 ± 5, consisting of 13 ± 2 meta-rule changes and 27 ± 3 rule changes. In Fig.2(a), the ordinate and abscissa denote the rate of correct trials and the number of trials from an occurrence of each of the two kinds of rule changes, respectively; the zero value on the abscissa denotes a trial when a new correct rule was applied, though the subject might be unaware of the change. The circle and triangle lines in Fig.2(a) correspond to meta-rule changes and rule changes, respectively. For each line, the error bar shows the standard deviation among all subjects. A comparison of these two time courses shows that subjects needed a significantly larger number of trials when they performed meta-rule changes than when they performed rule changes ($p<0.001$). In addition, behavioral profiles of each subject indicated that the subjects first explored within the current meta-rule, and then explored the other meta-rule (data not shown). These results suggest that the subjects tried to use a hierarchical rule structure to search for the correct rule quickly and efficiently.

Every behavior in the main task (other than excluded ones) can be classified into three kinds of conditions, MSW, RSW and "exploitation". Each subject was required to make prompt and accurate responses in the experiment, and their reaction time (RT, the time interval between presentation of a stimulus and initiation of a response to the stimulus) was examined. Fig.2(b) shows RTs for the four conditions. In this Figure, a bar and its corresponding error bar denote the mean RT and standard deviation over all subjects, respectively. The RT was significantly longer in MSW than in RSW ($p<0.05$), implying that MSW needs heavier cognitive processing than RSW. Since RTs between MSW and "exploitation" showed no significant difference, it is considered that cognitive processing inherent to RSW had been completed within the 6 sec period between the previous feedback presentation and the current stimulus presentation.

3.2 Imaging results

Brain areas significantly activated in the MSW condition and the RSW condition were compared. Group analysis showed significant activation of the left prefrontal lobe, especially in the inferior frontal gyrus (BA11, 45, 47) and insula (BA13), and these statistics are summarized in Table 2. Furthermore, we divided all voxels of the left inferior frontal gyrus into three areas, BA47, BA11 and BA45, and applied a time-course analysis to each of these three areas (Fig.3(a), lower panels). In each lower panel of Fig.3(a), the ordinate and abscissa denote the BOLD signal changing rate and the time elapsed since the feedback presentation in the previous trial, respectively. In the MSW condition, BA47 had a clear activation peak after feedback presentation, while BA11 and BA45 showed significant activation related to switch events but no distinct peaks.

We next compared brain images between the RSW condition and the "exploitation" condition, and the statistics of activated regions are also summarized in Table 2. Figure 3(b) shows the right cortical hemisphere and the areas activated in the RSW condition: the right superior frontal gyrus (BA10), right middle frontal gyrus (BA9/46,6) and superior parietal lobule (BA7,40). The time courses of signal intensities in these areas (Fig.3(b), lower panels) reveal that the superior frontal gyrus (BA10) showed a marked activation peak compared with the other conditions. Although BA9/46 also showed an activation peak in the RSW condition compared with the "exploitation" condition, this peak also occurred in the MSW condition. In BA6 of the middle frontal gyrus, although the overall activation level was higher in the MSW and RSW conditions than in the "exploitation" condition, the time courses resembled each other in all three conditions.

4 Discussion

4.1 Meta rule switch: higher order

Because there is a hierarchical structure of rules in our task, an appropriate search consists of a higher-order switch, i.e., a switch to a rule of the other meta-rule class, and a lower switch, i.e., a switch to a rule within the current meta-rule class. We consider this hierarchical structure introduces a 'context' to the exploration strategy for correct rules.

In the MSW condition, the left inferior frontal gyrus, consisting of BA11, 45 and 47, was significantly activated. Analysis of the three Brodmann areas revealed that each area has a different time course. BA47 showed a temporal increase of the signal intensity in MSW which was not observed in either RSW or "exploitation". In both the MSW and RSW conditions, subjects switched their rule because they were given 0 points as feedback in the previous trial. Since the activation of BA47 was observed only in MSW, however, this region was not involved in the detection of erroneous feedback. We also found that the activation in both BA11 and BA45 exhibited similar time courses in all three conditions; thus, BA47 is closely related to the meta-rule switch process in the left inferior frontal gyrus.

According to recent imaging studies, the left inferior frontal gyrus plays an important role in the retrieval process for episodic memory [5][10][16]. It was suggested that one of the cognitive processes in episodic memory retrieval is the systematic analysis of possible semantic relations between a stimulus and the known characteristics of potential information sources, which would be helpful for recollecting contextual details of the encountered stimulus [3][13]. To isolate this cognitive process, Dobbins et al. [5] used a task in which the subject recalled a word-class after having performed a semantic classification of many words. This study revealed that the left inferior frontal gyrus (BA47) was concerned with the information retrieving process for word stimuli. Other studies have also shown that almost the identical region was involved in recollections related to the recognized stimulus [8][15]. In our task, we think that meta-rules (higher-order components) are intensive information representations of lower-order rules. Thus, restricting the search space based on meta-rules may exploit a cognitive process that performs efficient information retrieval for episodic memory, i.e., contextual information. Although Dobbins et al.'s task was a linguistic one while ours is a diagrammatic one, and they have different modalities, these results suggest that the left inferior prefrontal gyrus plays an important role in manipulating aggregated information.

4.2 Rule switch: lower order

In the RSW condition, we found that the right superior frontal gyrus (BA10) and right middle frontal gyrus (BA9/46,6) were significantly activated.

A previous study using a categorization task, in which the subject was required to search for a hidden correct rule by trial and error, suggested that the right superior frontal gyrus (BA10) was involved in seeking rules which was induced by changing the correct rule [17]. However, this region was not active when subjects sought a correct rule in WCST [9][12]. In both tasks, subjects had to switch rules based only on feedback; hence, they knew it was necessary to switch rules if they received a 'false' feedback. In the categorization task, each stimulus could be compatible with multiple rules. If a false feedback was given, therefore, the subject could eliminate not only the used rule but also several other rules, whereas a true feedback did not necessarily indicate that the used rule was correct. Thus, the subject would maintain more than one possible rule candi-

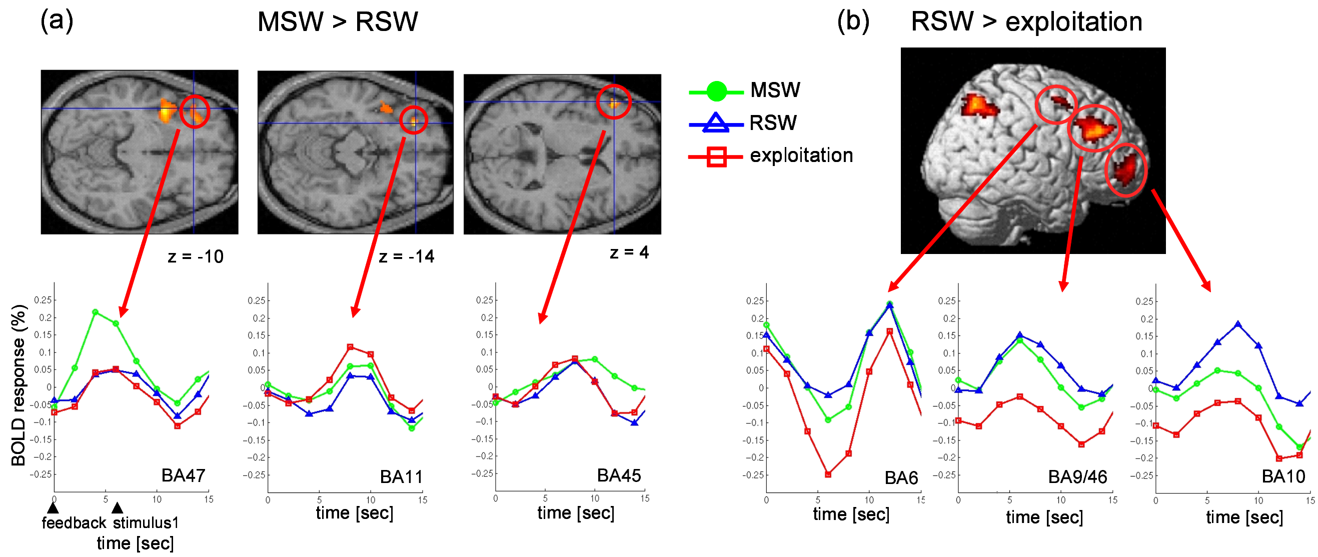

Figure 3. Imaging analysis. (a) Activation specific to meta-rule switching in comparison to rule switching (upper panels) and time courses of the activated regions (lower panels). (b) Activations specific to rule switching in comparison to exploitation (upper panels) and time courses of the activated regions (lower panels).

date. In the WCST, however, feedback was given according only to the rule used by the subject. If a false feedback was given, therefore, the subject simply removed the used rule from the candidates. In contrast, probabilistic feedback was given in our task. If an unfavorable feedback was given, the subject would be expected to reduce the probability (likelihood) that the used rule was correct, and to increase the probability of the other rule candidates being correct; if a favorable feedback was given, the subject would be expected to perform the contrary. The common feature of the categorization task and our task, in both of which activation of BA10 was found, is that two or more rule candidates should be handled in response to a given feedback because feedback in both cases was not explicit. BA10 may be activated when the subject estimates the hidden correct rule from given feedbacks and updates the likelihoods of rule candidates so as to redefine the rules' priorities. Moreover, according to our time-course analysis of this region, a more prominent activation was found in RSW than in MSW (although the activation was larger in MSW than in "exploitation"). This result can be interpreted as follows. In RSW, likelihoods can be updated because removal of a used rule reduces the number of possible rule candidates. In MSW, in contrast, removal of a used rule does not reduce the number of possible rule candidates because it does not yield any knowledge on rule candidates belonging to the other meta-rule class; thus, there is no need to update the prioritized weights.

In the lower-order RSW, the right dorsolateral prefrontal cortex (BA9/46) was significantly activated. This region was previously found to be activated in WCST regardless of whether a true or false feedback was given [12]. Although subjects with lesions in this region could discover the first correct rule, they could not adapt to changes in the correct rule because they clinged to this rule [4][11][14]. It is therefor thought that BA9/46 is involved in monitoring and/or updating the information stored in working memory. In our experiment, the activation intensity of this region in the "exploitation" condition was lower than that in the MSW and RSW conditions; this is consistent with current understanding as outlined above.

4.3 Information processing hypothesis

Time-course analysis of significantly activated regions indicated that the timing of activation was different in each of the three activated regions in the prefrontal cortex. Based on these results, we suggest a brain information processing model which explains the behaviors of rule switching.

The time courses of signal intensities in the three regions, discriminated by the three behavioral conditions, are shown in Fig.4. These different time courses can be interpreted as meaning that the subject first limits the searching space in BA47, then loads rule candidates in working memory in

Table 2. Statistics of significantly activated regions

Condition	Region	Left / Right	Brodmann	Talairach[x,y,z]	*Z*-value
MSW > RSW	Inferior PFC	L	11/45/47	-28, 38, -14	3.52
	Extra-Nuclear	L	13	-38, 5, -7	3.99
	Insula	L	13	-36, 17, -1	3.03
	Superior Temporal	L	22/38	-45, 5, -8	2.78
RSW > exploitation	Fronto-Polar PFC	R	10	32, 58, 3	3.86
	Dorsolateral PFC	R	9/46	50, 20, 24	4.39
	Middle Frontal Gyrus	R	6	32, 2, 50	3.95
	Precuneus	R	7	6, -64, 46	5.54
	Precuneus	L	7	-6, -61, 56	4.44
	Superior Parietal	R	7	30, -58, 49	4.38
	Inferior Parietal	R	40	42, -54, 45	3.77
	Supramarginal Gyrus	L	40	-40, -43, 37	4.97

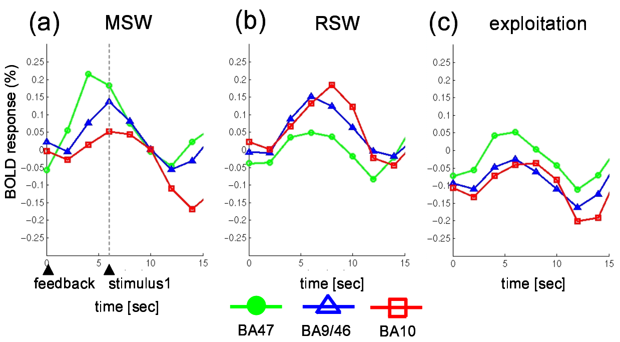

Figure 4. Time couse of MRI signal intensities in each of the event conditions. (a) Meta-rule switching; (b) rule switching; (c) exploitation.

BA9/46, and finally determines the priorities of these candidates in BA10. In the MSW condition (Fig.4(a)), the activation increase in the left inferior frontal gyrus (BA47) was followed by activation in the right dorsolateral prefrontal cortex (BA9/46), whereas the fronto-polar prefrontal cortex (BA10) did not show any distinct activation. Since the subject arbitrarily selects one rule from the loaded candidates, activation of BA10 is not required because of the absence of any priorities among the loaded candidate rules. In the RSW condition (Fig.4(b)), activation of BA47 does not occur because the searching subspace is already determined. The subject first refers to the candidates held in BA9/46, and the priority of each candidate is then assigned in BA10. In the "exploitation" condition (Fig.4(c)), none of the regions are markedly activated because the sub-processes above are not necessary.

5 Concluding remarks

We have designed a Multi Feature Sorting Task in which the behavioral rules have a hierarchical structure, and conducted an fMRI experiment using this task. In our task, subjects were required to apply two kinds of rule switches which correspond to the retrieval of different hierarchies. The left inferior frontal gyrus (BA47) was specifically activated in higher-order meta-rule switches. It is considered that this region restricts the searching space by handling intensive information, in agreement with previous studies suggesting that BA47 is involved in recollecting information from episodic memory; this recollection function is useful for limiting rule candidates, as required in our task. The right fronto-polar prefrontal cortex (BA10) was specifically activated in lower-order rule switches; this region may thus be involved in prioritizing rules, in agreement with previous work suggesting that BA10 is involved in predictive rule switching tasks. Our results suggest that humans can effectively represent information as a hierarchical rule structure which can be operated efficiently by incorporating contextual information.

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