The neural correlates of rule implementation and attentional bias in the task-cuing paradigm

Yiquan Shi

SIGILL: UNIVERSITAT: LUDOVIC: MAXIM:

The neural correlates of rule implementation and attentional bias in the task-cuing paradigm

Inaugural-Dissertation
zur Erlangung des
Doktorgrades der Philosophie an der
Ludwig-Maximilians-Universität
München

vorgelegt von
Yiquan Shi

aus
München

Referent: Prof. Dr. Torsten Schubert, Department für Psychologie, LMU
Korreferent: Prof. Dr. Hermann Müller, Department für Psychologie, LMU

Tag der mündlichen Prüfung: 22. Dezember 2009

Table of Contents

CHAPTER 1

General background and research questions

1.1 Executive control in the task-cuing paradigm

The executive control system is a supervisor system which can guide, modulate and coordinate other cognitive processing to achieve certain task goal. It plays important role for successful goal-directed behavior especially in situations with changing task contexts. Particularly in these changing task contexts, the requirements of flexibly activating appropriate task rule is high. Thus the executive control for rule implementation is needed. Moreover, efficiently focusing of attention to the task relevant characters but ignoring the task irrelevant characters is also highly required. Thus executive control for bias of attention is needed in this situation.

A paradigm, called task-cuing paradigm, is suitable to investigate the executive control in the changing task contexts (e. g., Allport 1994; Meiran 1996; Rogers & Monsell 1995). In this paradigm, subjects are required to rapidly switch between two different discrimination tasks (e. g., gender discrimination and color discrimination for colored face picture). The current task can either be the same or different to the preceding task, which is referred to as repetition or switch condition respectively. Before the appearance of the target, a task-cue is presented to indicate the upcoming task, thus permitting preparation for that task and making it possible to temporally dissociate task preparation from task execution (e. g., Meiran 1996). It has been shown that in the task-cuing paradigm, participants' performance benefits from a prolonged cue-target interval (CTI), which points to the ability of successful task preparation guided by executive control (Meiran 2000; Rogers & Monsell 1995).

Particularly in this paradigm, the frequently change of task leads to ongoing changes of the relevant task representations including the task relevant feature (e. g., face or color) and rule knowledge. Correspondingly, the bias of attention (Meiran 2000; Monsell 2003; Rogers & Monsell 1995) and the rule implementation (Mayr & Kliegl 2000; Rogers & Monsell 1995, 2003; Rubinstein et al. 2001) are claimed and examined to be critical cognitive components for task representation (or configuration) in this paradigm (see Fig. 1.1). My present study aimed to investigate the neural correlates of these two critical cognitive processing: rule implementation and bias of attention, in changing task contexts.

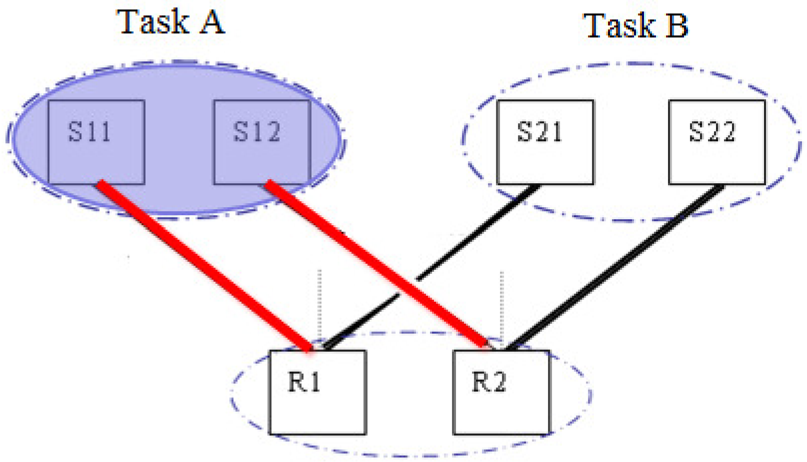


Figure 1.1: If the current task is task A, attention should be biased to category A rather than B, and the task rule of task A rather than B should be activated. S11 and S12 are the two features of task A; S21 and S22 are the two features of task B. R1 is the corresponding response to both S11 and S21; R2 is the corresponding response to both S21 and S22.

1.2 Research questions

Presumably, the activation of such attentional bias and rule implementation are parts of a more general mechanism of task preparation, which includes the prior activation of neural modules necessary for behavior and starts long before the manifestation of the overt behavior (Gollwitzer & Sheeran 2006; Monsell 2003; Rubinstein et al. 2001;).

A number of studies were conducted to investigate the neural basis of the broader mechanisms of task preparation (Brass & von Cramon 2002, 2004; Gruber et al. 2006; Luks et al. 2002; MacDonald et al. 2000; Sohn et al. 2000). These studies on task preparation showed a large scare of cortical regions including the lateral prefrontal cortex (LPFC), the medial frontal cortex (MeFC), pre-motor regions, and parietal regions to be part of a network that seems to come into play when participants prepare for an upcoming sensory-motor task.

On one hand, intraparietal cortex and superior frontal cortex are identified to be critical for attentional control by several fMRI studies (e g., Corbetta et al. 2000, 2002, 2005; Serences et al., 2001, 2004; Serences & Yantis 2007). Notice that, the foci of attentional control locate within the networks of task preparation. This finding fits well with the hypothesis that attentional bias is part of the general task preparation. On the other hand, the neural mechanisms of task rule activation in changing task contexts are still not clear yet. Therefore the first fMRI experiment of this study was conducted mainly to investigate whether regions specific to the mechanisms of task rule implementation can be found (presumably) within the task preparation networks.

Again for the bias of attention, it was assumed that the top-down control biases the “bottom-up” sensory processing via amplifying the neural representation in some corresponding feature specific posterior regions (e g., Desimone & Duncan, 1995; Kastner & Ungerleider, 2000). And this opinion was supported by several preceding findings (e g., Corbetta et al. 2005; Serences et al., 2001, 2004; Serences & Yantis 2007). However, if the preparatory attentional control also biases sensory processing through a similar way is still lacking of investigation. Therefore the second fMRI study was conducted mainly to investigate if preparatory attentional control could bias sensory processing via the modulation to the posterior feature specific regions' activity.

1.3 Method of isolating cue period and target period neural activity

This study aimed to isolate the neural correlates for task rule implementation from the brain network of general task preparation, and to find the modulation in the posterior brain regions' activity in the task preparation period. Considering the processing in the target period (during task execution, i.e. after the target was presented) are temporally close to the processing in the cue period (during task preparation, i.e. in the interval between the presenting of cue and target). Particular method is needed for the adopted methodology, functional magnetic resonance image (fMRI), to dissociate the task preparation-related and task execution-related neural activity. . Studies concerned with understanding the neural mechanisms of task preparation have often used the task-cuing paradigm in combination with an event-related fMRI design (Brass & von Cramon 2002, 2004; Gruber et al. 2006; Luks et al. 2002; Sohn et al. 2000). Earlier neuroimaging studies investigated preparation-related activity by analyzing the fMRI activity during very long CTIs (e.g., up to 12.5 s) and, therefore, their findings may have been compromised by memory load confounds (Luks et al. 2002; MacDonald et al. 2000; Sohn et al. 2000).

More recent studies isolated task preparation-related activity by measuring neural activity separately for so-called cue-only trials, cue-target trials, and null-events in the task-cuing paradigm (Brass & von Cramon 2002, 2004). While on cue-only trials, there is no target following the cue, on cue-target trials a target requires the execution of the task, and the null-event represents a baseline condition without any cue and target information. Because participants do not know in advance whether or not a target will follow the cue, they have to prepare for task execution on every type of trial, both on cue-only and on cue-target trials (see also Corbetta et al. 2000; Weissman et al. 2005). This allows for a measurement of preparation-related activity during the processing of cue-only trials.

With the use of cue-only trial design, Brass and von Cramon (2002) contrasted activation in cue-only trials and in null-events and found a fronto-parietal network to be related to task preparation. In particular, this network included regions in the dorsolateral prefrontal cortex (DLPFC), e.g., near the inferior frontal junction point (IFJ), regions surrounding the intraparietal sulcus (IPS), in the dorsal premotor cortex and in the pre-supplementary motor area (pre-SMA) of the medial frontal gyrus.

The fMRI Experiments 1 and 2 in the present study adopted the cue-only trial design and the task-cuing paradigm in order to find the neural correlates of task rule implementation and the possible attentional modulation to feature specific posterior regions respectively.

In particular, the research aim of fMRI Experiment 1 was achieved by the applying of a new kind of cue called “rule-cue”. In the rule-cue display, not only the task type information but also the rule of the current task (a set of S-R associations) were explicitly presented. Note that, before the formal experiment, participants have received enough practice which can make sure the task rules have been remembered well. So I expected the participants did not use the explicit rule information in the rule-cue to learn the task rule (e g., consolidate their memory of task rule or obtain the task rule better), rather they used this information to implement the task rule. This hypothesis was supported by a behavioral experiment, Experiment 3 of this study. It will be introduced after the description of the two fMRI experiments.

Since the rule-cue can implement the task rule more efficiently than the task-cue which supplies explicit task type information only, the neural activities in these two cue conditions were compared in Experiment 1 to identify the neural correlate of rule implementation.

1.4 Introduction of fMRI Experiment 1:

The neural mechanisms of task rule implementation

According to Miller (2001) rule knowledge is stored in the prefrontal working memory and it contains knowledge about the stimuli, the behavioral responses, and about the context of the situations in which a particular rule has to be applied. As introduced above, the activation of such rule representations could be part of a more general mechanism of task preparation, which refers to a large scare frontal-parietal network. And the aim of this present experiment is to further find the unequivocal neural correlates of task rule implementation.

Although the findings provided a number of valuable insights into the functional neuroanatomy of task preparation, they are not unequivocal regarding the neural correlates of task rule activation. This is so because a task-cuing paradigm like that in Brass and von Cramon (2002) does not permit the mechanisms of activating the specific task rules to be distinguished from rather general task preparation (see also Ruge et al. 2009). The presentation of the cue informed participants about the task they had to perform later upon the presentation of the target. If the time was sufficient and the participants intended to do so, they could either activate the current task rule or, alternatively, they could wait with the activation of the task rule until the presentation of the imperative target. Thus, depending on participants' strategy, either to prepare the task rule early upon the presentation of the cue or only later upon the presentation of the target, the point in time when the task rule was activated was not sufficiently controlled.

For the present study, a so-called rule-cue was designed, in order to investigate rule-related activation in a task-cuing paradigm. This rule-cue differs from the task-cue in earlier studies because it conveys explicit information about the type of task and, in addition, about the corresponding task rule (e. g., in a color discrimination task use left key for red and right key for yellow color). Thus, while a task-cue (the sort of cue used in earlier studies) conveys only general information about which task to perform, the rule-cue provides also specific information about task rules, e.g. the stimulus-response (S-R) mapping, on the upcoming trial (task-and-rule information). By administering the rule-cue randomly mixed with task-cues, this experiment aimed to trigger processes related to the activation of the specific task rules during task processing.

In particular, Chinese participants attended Experiment 1. They were presented with either a color or a gender discrimination task, with the particular task specified by the presentation of a cue before the target stimulus. In the rule-cue condition (Fig. 1.2, left panel), the Chinese symbols "颜色" (for color) or "性别" (for gender) were displayed to indicate the upcoming task, and also the specific instructions of its S-R mapping rule. For example, if the task was gender discrimination, the symbols "男" (for male)"女" (for female) were presented above the corresponding response keys (e g., “male” was shown above the left key and “female” above the right key).

In the task-cue condition, the symbols "颜色" (color) and "性别" (gender) were also used to indicate the next task, whereas there was no specific information about the task rule (see Fig. 1.2, right panel). Instead, only non-informative words "按 键" (press key) were presented below the task-cues, in order to make the cue display similar to that in the rule-cue condition.

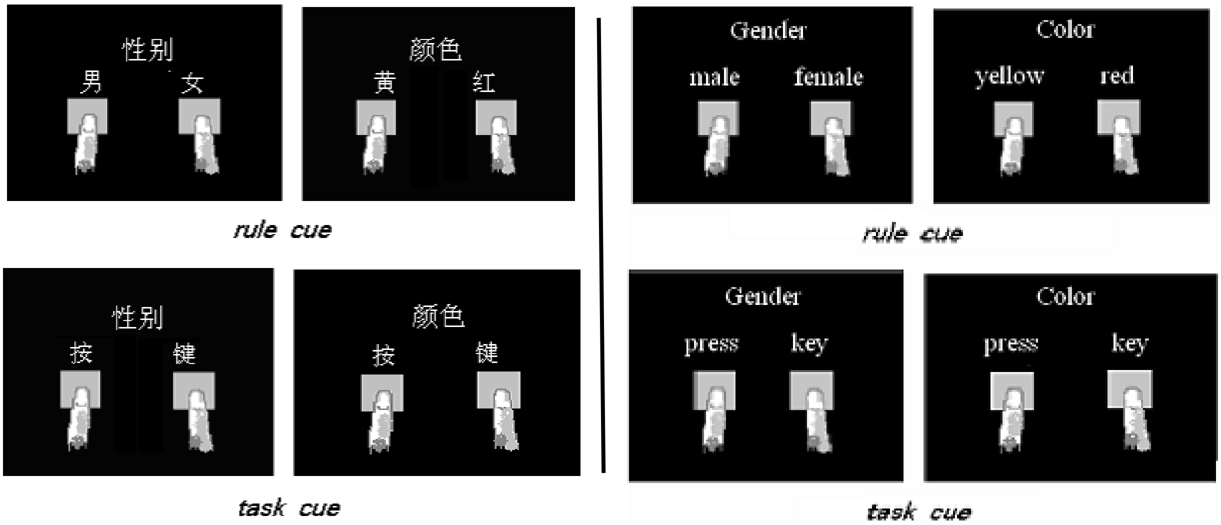


Figure 1.2: Illustration of the rule-cue and task-cue displays (left panel) and their English translation (right panel). In the rule-cue and the task-cue conditions, the current task was indicated by the words “颜色” (color) and “性别” (gender), respectively. In the rule-cue condition (upper row), additional information indicated the assignments of the response keys to the stimulus

Similar to Brass and von Cramon (2002), cue-only trials (Fig. 1.3, right panel), null-events, and cue-target trials (Fig. 1.3, left panel) were presented. While an analysis of the cue-only trials allows for detection of preparation-related activation that is elicited by the cues (rule and, respectively, task-cues), target-related processes are revealed by contrasting activity between cue-target and cue-only trials (e g., Brass & von Cramon 2002; Weissman et al. 2005). Because the activation in cue-target trials consists of activation related to cue- and to target-processing, subtracting the cue-related activation from the activation in cue-target trials will left over the target-related activation only.

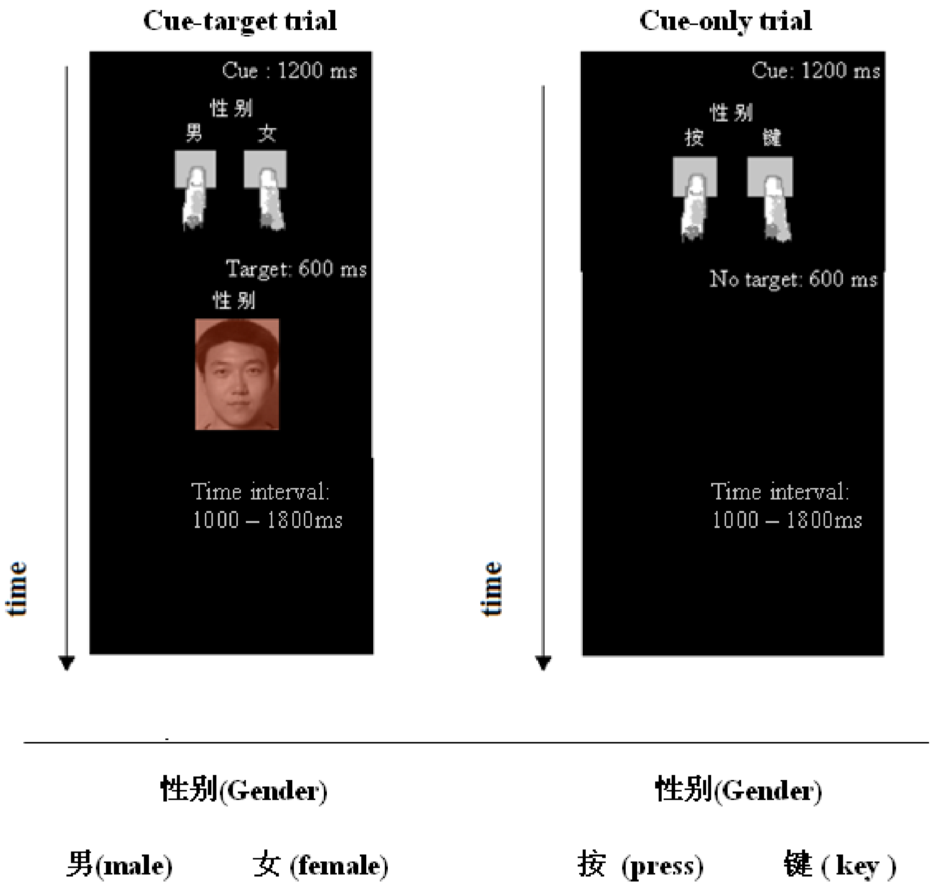


Figure 1.3 : Illustration of the task situation. Upper part: Left panel shows a cue-target trial (example for the gender discrimination task). Right panel shows a cue-only trial (example for gender discrimination task). The lower part of the figure represents the cue displays and their English translation. The cue could either be a rule-cue (left) or a task-cue (right), (for details see

The distinction between rule-cues and task-cues permits rule-related neural activity to be analyzed in the following manner. First of all, the experiment expects a significant performance benefit from the presentation of rule-cues compared to task-cues, and rule-cues can evoke stronger cue-related activation than task-cues, specifically, on cue-only trials. The reason for the latter hypothesis is that, in the rule-cue condition, the cue provides explicit rule information and this information may be activated with the cue presentation. By contrast, in the task-cue condition, participants may postpone at least part of the rule activation processes until later, for example, up to the time where the target is expected to appear. And even if activation of the rule is not postponed, it may be less effective because the cue provides no explicit information as to the precise task rule. Consequently, rule-related activation should be manifest during the preparation period on cue-only trials in terms of an increased amount of activity under the rule-cue, compared to the task-cue, condition (see the orange dotted oval in Fig. 1.4).

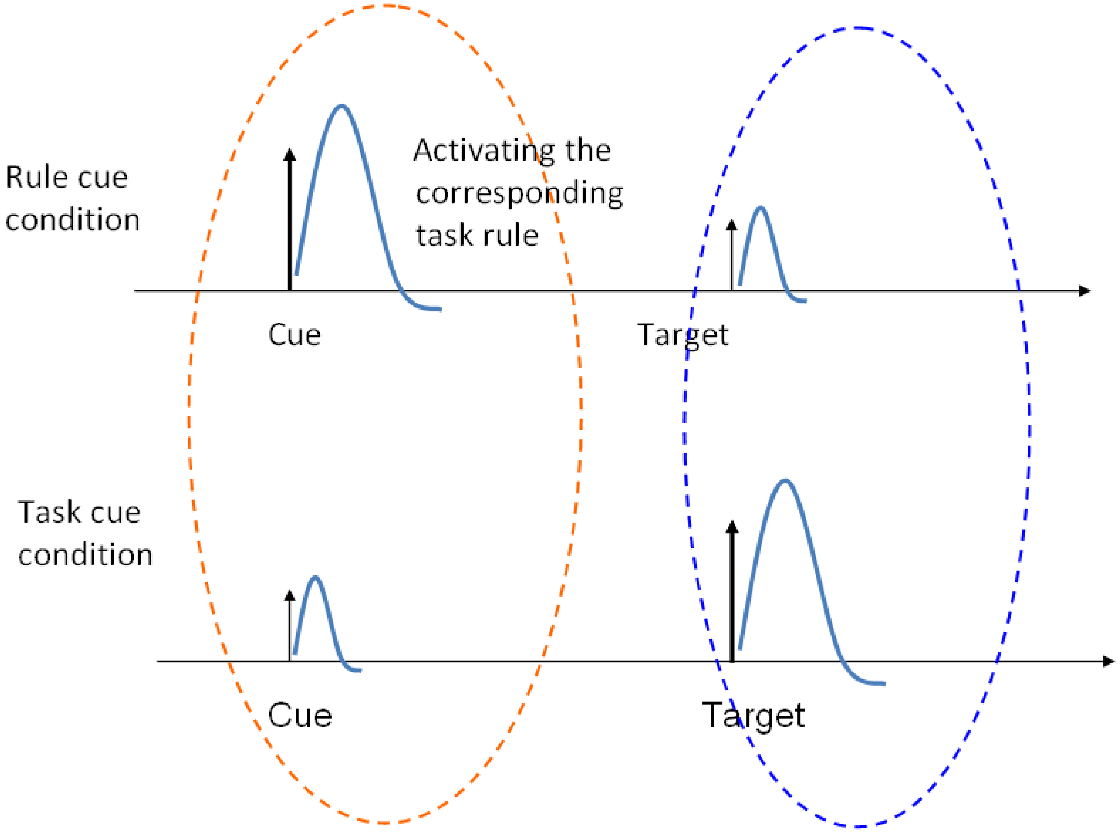


Figure 1.4: The expected activation pattern in the rule-related regions

The converse pattern (of activation in rule-cue and task-cue conditions) may be expected when considering the rule-related activation that emerges after target presentation on cue-target trials, i.e. during task execution. It is reasonable to assume that, if participants failed to activate the (complete) task rule right upon cue presentation, they must activate the necessary S-R mapping rule following target presentation (Gruber et al., 2006). This would be consistent with Gruber et al. (2006) who analyzed the neural activity under conditions of short vs. long cue-target intervals (CTIs) in a task-cuing paradigm. While the time for preparing the upcoming task was sufficient after cue presentation with long CTIs, it was insufficient with short CTIs. The latter led to the postponement of (at least parts of) the preparation processes until after target presentation, as indicated by an increased amount of neural activity in preparation-related brain regions under conditions of short compared to the long CTIs (Gruber et al. 2006; see also Brass & von Cramon 2002). In analogy to these findings, postponed rule activation in the task-cue condition compared to the rule-cue condition was expected. This should lead to greater activation in rule-related brain regions under task-cue, compared to the rule-cue condition upon target presentation on cue-target trials (see the blue dotted oval in Fig. 1.4).

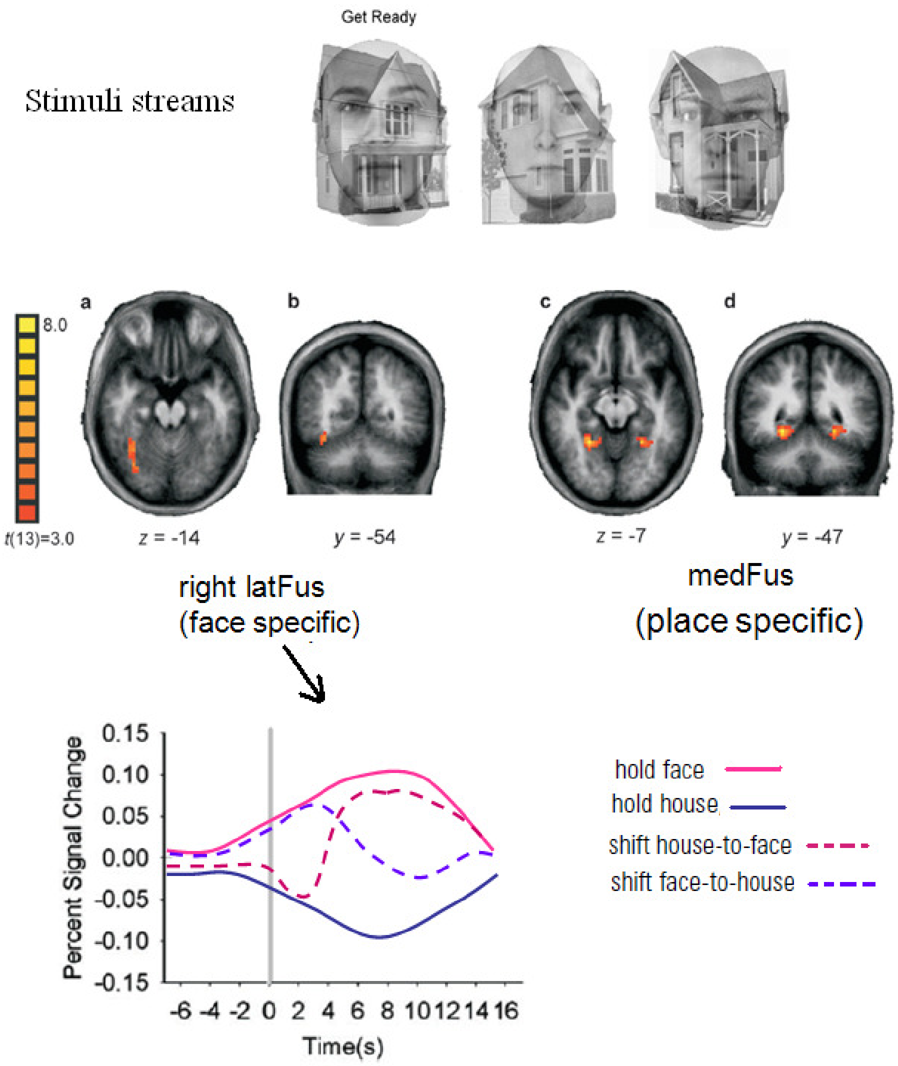
In sum, the expectation include stronger neural activity related to task rule activation in the rule-cue compared to the task-cue condition during the preparation period, and stronger activity in rule activation-related regions during task execution in the task-cue compared to the rule-cue condition. The common neural substrate in these two comparisons, thus, represents those brain regions which are important for the mechanism of task rule activation either in the task preparation or in the execution period. A method called conjunction analysis is suitable to find the common activation of different comparisons. This experiment adopted the conjunction analysis to find the common neural substrate about the corresponding contrasts (i.e., preparation period (rule-cue minus task-cue), and execution period (task-cue minus rule-cue)).

1.5 Introduction of fMRI Experiment 2

The preparatory attentional modulation to the posterior brain regions

Several studies (e g., Dehaene et al. 2003; Kanwisher et al. 1997; Serences et al., 2001; Tootell et al., 1995; Zeki et al., 1991) have shown that there are several stimulus-specific posterior brain regions who are sensitive to the presenting of certain specific stimulus (e g., face, or house, or motion, or number) rather than other stimulus.

In spite of the physical power of stimulus, the response of such posterior brain regions to their specific stimuli can be modulated by attention. This had been shown by a study of Serence et al. (2004). In that study, two spatially overlapped streams of face stimulus and house stimulus were displayed in the screen (see Fig. 1.5, upper panel). A verbal command was given to instruct participants attending to either houses or faces and maintaining attention on the currently attended object stream until the next command. Attentional modulation was found: an increased response in the face specific region (right lateral fusiform) when participants attended to faces (see Fig. 1.5, lower panel), whereas an increased response in the place specific region (bilateral median fusiform) when participants attended to houses (Serences et al. 2004).



Adapted from Serences et al. (2004 ; Cerebral cortex)

Figure 1.5: Upper panel: the stimuli streams of faces and houses. Middle panel: the localization of face specific (right lateral fusiform) and place specific posterior brain regions (left and right medial fusiform). Lower panel: the attentional modulation was found in the face specific region.

Another interesting characteristic of these specific regions is that even when participants did not look at the stimulus, these regions could be activated by the imagination or the working memory maintenance of their specific stimulus (O'Craven &Kanwisher 2000; Lepsien & Nobre 2007).

In the cued task switch paradigm, after the presentation of the cue, the participants tend to prepare the task in advance in order to improve their performance; the attentional control was assumed to be an important component of such task preparation (Meiran 2000; Monsell 2003; Rogers & Monsell 1995). Considering the fact that region could activate without the explicit presentation of the stimuli, it seems plausible to assume that the preparatory attentional control may lead to a modulation to the posterior specific regions. However, the investigation for this preparatory attentional modulation and its support evidences are rare.

One relevant finding supporting this assumption was observed by Wylie et al.'s study (2006). Here, participants responded to a colored rotating bar, either discriminated the color of the bar or judged the bar's rotating speed is slow or fast. Cue was given to inform about the current task. In the preparation period, modulation was found in the color specific region but not in the motion specific region. This finding at least partially supports the hypothesis which implies that attentional bias can pre-activate the task relevant representations in the posterior specific regions. For the silent of motion specific region in speed task preparation period, it was explained the participants did not efficiently prepare the speed task. One of the possible reason might be the motion discrimination task dose not encourage preparation. For example, Shulman et al (2002a) either did not find motion-selective activity in middle temporal area (MT, specific for motion) when subjects were verbally cued to attend to motion (Shulman et al., 2002a).

Moreover, the factor of balance of task difficult was considered, It has been proposed that, in the changing task context, if the two tasks are not balanced in difficulty, in order to perform the non-dominant task well, participants may have the tendency to inhibit the dominant task. This inhibition could persist into next trial (Allport et al., 1994). And such inhibition processing might depress the activity in the posterior brain region, which does not fit with the aim of this experiment.

Thus in this present study, in order to encourage efficient task preparation in both tasks, two tasks with balanced difficulty were planned to use, and no motion related task was considered.

In the current experiment, a gender and a number discrimination task were adopted (male/female; bigger/smaller than five). The corresponding regions of interest (ROIs) are the fusiform face area (FFA) (Kanwisher et al. 1997) and a region in the horizontal segment of the intra parietal sulcus (IPS). Note that, the IPS processes multitude information in its different parts, but the region in the horizontal segment is specific to the representation of number. It is systematically activated whenever numbers are manipulated, independently of number notation (Dehaene et al. 2003). In the present study, this region was called IPS number region (IPSnum).

A preliminary behavioral experiment was conducted and showed that the selected two tasks are not significantly different in difficulty thus efficient task preparation should take place for both of these two tasks (see supplementary material 1), therefore pre-activation was expected in the FFA if the task was gender discrimination and it was expected in the IPSnum if the task was number discrimination.

This experiment tried to find the evidence for the hypothesis that the preparatory attentional control can bias sensory processing via amplifying the activity of the task-relevant stimulus-specific brain region. A cue-only trial design was used in fMRI Experiment 2 to isolate the neural activity in task preparation period. The modified cued task switching with the use of rule-cue was adopted. Both the rule-cue and task-cue provide the task type information which allows preparatory attentional biasing, therefore the corresponding modulation to the stimulus specific region was expected in both of the two cue conditions:

i.e., the increased activity in FFA in the preparation period of face task and the increased activity in IPSnum in the preparation period of number task.

Contrary to Experiment 1, German participants attended this Experiment 2. There might be cultural differences in strategy use and functional neuroanatomy of task rule implementation. Therefore, it is interesting to check if the finding in Experiment 1 could be replicated. This was a further aim of the present Experiment 2.

Moreover the present Experiment 2 can also check if the presentation of task rule information is accompanied by activity changes in posterior sensory brain regions (larger activity in the face specific region in the preparation period if the task is indicated by a rule-cue than a task-cue; and similar or number task) or not.

In particular, in the main task, participants were presented with either a number or a gender task, with the particular task specified by the presentation of a cue before the target stimulus. In the rule-cue condition, the German symbols "ANZAHL" (for number) or "GESICHT" (for face) were displayed to indicate the upcoming task, and also the specific instructions of its S-R mapping rule. For example, if the task was gender discrimination, the symbols "MANN" (for male)"FRAU" (for female) were presented above the corresponding response keys (e g., “male” was shown above the left key and “female” above the right key).

In the task-cue condition, the symbols "ANZAHL" (number) and "GESICHT" (gender) were also used to indicate the next task, whereas there was no specific information about the task rule. Instead, only non-informative words “PRESS" (press key) were presented below the task-cues, in order to make the cue display similar to that in the rule-cue condition.

Similar to fMRI Experiment 1, cue-only trials, null-events, and cue-target trials were presented. While an analysis of the cue-only trials allows for detection of preparation-related activation that is elicited by the cues (rule and, respectively, task-cues) in the face or number task, target-related processes are revealed by contrasting activity between cue-target and cue-only trials.

Besides of the main task, a localization task was conduct to identify the regions of interest (ROIs) (i.e., face specific and number specific region) for each individual subject. The activity of the face and number specific regions in the main task were analyzed in order to find the preparatory modulation of attention. i.e., the increased activity in face specific region in the preparation period of face task and the increased activity in number specific region in the preparation period of number task.

In sum, this experiment aimed to find the evidence for the hypothesis that the preparatory attentional control can bias sensory processing via amplifying the activity of the task-relevant stimulus-specific brain region. For this aim, gender discrimination and number discrimination tasks were selected because they both refer to specific posterior brain region (i.e., FFA and IPSnum) and they are balanced in task difficulty (good for efficient preparation in both tasks).

1.6 Introduction of Experiment 3:

The rule-cue was expected to activate the task rule more sufficiently in the preparation period. However, one might argue that the rule-cue could facilitate the rule acquisition as well as rule implementation. Therefore one might expect that the participants may also learn the task rule from the displays of the rule-cues whereas no such learning processing occurred in the task-cue condition because the task-cue displays supply no rule information. If this is really the case, the rule-related finding in Experiment 1 and 2, which was resulted by the comparison between neural activity in the rule-cue and task-cue conditions, might be confounded by some learning effect.

I suggest that such learning of task rule from the rule-cue displays only take place when the rules have not yet been obtained well. Human, unlike the monkey or chimpanzee, the process of achieving a good acquisition of task rules was expected to be not time consuming, only few trials should be enough for obtaining simple rule sets in the present study. Therefore the rule-related activation found in Exp 1 and 2 should not confounded with learning effect, because participants received enough practice before the formal experiment. In order to test this hypothesis, Experiment 3 was conducted. Considering Experiment 1 adopted Chinese participants and Experiment 2 adopted German participants, both Chinese and German participants were adopted in Experiment 3. I expect the hypothesis works for both Chinese and German participants.

The setting of rule transition factor

A task environment with unstable task rule was designed in this behavioral experiment. Participants have to perform either gender discrimination or number discrimination (like in the normal task-cuing paradigm); however the task rules are unstable. The task rule of face discrimination could either be male-left, female-right or the reversed; the task rule of number discrimination could either be bigger than five-right, smaller than five-left or the reversed.

Before every block which contains 10 trials, task rules (for face and number task) are displayed on the screen for a relatively long period (i.e. 5.5s). Participants were instructed in advance these rules were the rules for the following block and they had to remember the rules. If the current task rules are the same with the rules in the preceding block, the current block is a rule repetition block. Otherwise, the current block is a rule switch block. Moreover, within a block, each task could either be guided by rule-cue or task-cue, thus resulting rule-cue block or task-cue block.

Note that, the re-acquisition of rules is needed in the first few trials of rule switch block. After the 5.5 seconds presenting of the rules display, participants can explicitly learn the task rules from the cue displays in the rule-cue block but not in the task-cue block. , correspondently, part of the rule cue benefit should come from the rule cue facilitation to the new rule's acquisition. In addition, the rule cue should also refer to a better rule implementation process than the task cue; this causes another part of rule cue benefit.

Whereas in the rule repetition block, the rule sets have been learned well already, thus no spaces for the rule cue facilitation to the rule acquisition processing anymore. But the rule cue facilitation to the rule implementation still exists; it produces rule cue benefit per se.

Taking them together, for the first few trials of block, because the rule cue benefit was contributed by rule cue facilitation to rule acquisition and rule implementation both in the rule switch block, whereas produced by rule cue facilitation to rule implementation only in the rule repetition block. More rule cue benefit was expected in the rule switch block than in the rule repetition block.

However, for the rest trials in a block, even it is a rule switch block, the task rules should been acquired well already. Therefore the rule cue benefit should be produced by rule cue facilitation to rule implementation only no matter the block is a rule repetition or rule switch block. Thus for the rest trials of blocks, there should be identical rule cue benefit in the rule switch and rule repetition block.

In sum, for the first few trials of blocks, more rule cue benefit was expected in the rule switch blocks than in the rule repetition blocks. Whereas for the rest trials of blocks, identical rule cue benefit was expected in the rule switch and rule repetition blocks.

CHAPTER 2

fMRI Experiment 1

2.1 Research aim and expectations

To isolate the neural correlates for task rule activation from those related to general task preparation a new kind of cue called "rule-cue" was created and applied in the cued task switching paradigm. While the task-cue represents merely information about the task type, the rule-cue represents information about the task type and, in addition, explicit information about the task rule (i.e. the set of S-R correspondences). The rule-cue was expected to activate the task rule more sufficiently in the preparation period (main contrast 1: cue period (rule-cue mins task-cue)), whereas in the task-cue condition, part of the task rule activation was expected to be postponed into the task execution period, i.e. after the target was presented (main contrast 2: target period (task-cue mins rule-cue)). The common neural substrate in these two contrasts, thus, should represent those brain regions which are important for the mechanism of task rule activation either in the task preparation or in the execution period.

2.2 Method

Subjects

Fifteen right-handed, healthy students of Peking University (recruited by advertisement in the campus Bulletin Board System) participated in the study. Six participants were female; participants' ages ranged between 20 and 26 years, and all had normal or corrected-to-normal vision. Prior the fMRI scanning session, they gave informed consent about the investigation according to the Helsinki guidelines and the approval of the Academic Committee of the Department of Psychology, Peking University. Participants were paid 50 yuan (about 5 Euros) for their service.

One participant's response error rate was more than 20 %. Hence this participant's behavioral and fMRI data were removed from the data set. There was also a loss of the behavioral data from one participant, due to data recording error. Thus, ultimately, 14 participants' image data sets and thirteen participants' behavioral data sets were available for analysis.

Design

Paradigm and procedure. The task to be performed by the participants was either color discrimination or gender discrimination. Each trial began with the presentation of a cue for a fixed duration of 1200 ms, which could either be a rule-cue or a task-cue (see Fig. 1.1). Both cues displayed an instruction for the upcoming task; however, a precise instruction about the required task rule was provided only in the rule-cue condition (for more details, see Fig. 1.2). On cue-only trials (n = 160 trials, of which 80 presented a rule-cue and 80 a task-cue), there was no target following the cue offset, but only a black screen that lasted for 600 ms, and there was no need for participants to make a response (Fig. 1.1, right panel).

In contrast, on cue-target trials (n = 280, of which 140 presented a rule-cue and 140 a task-cue), the cue was followed by a colored face picture that was presented for 600 ms; during this period, the task-cue instruction remained visible on the screen (above the target picture) by presenting the words ‘gender’ or ‘color”, so as to reduce participants’ working memory load for maintaining the task goal in the two conditions. Importantly, the information presented during the execution period concerned only the task information and not the rule information because the symbols ‘press key’ and the symbols illustrating the rule information were not presented during the execution period (see Fig. 1.1, left panel). Participants were to respond to either the color or the gender of the face depicted in the target display, depending on the instruction of cue. Participants made two-alternative forced-choice responses using either their left or their thumbs, with response sets counterbalanced across participants. After the offset of the target picture, a black screen was presented for a variable interval of 1000, 1200, 1400, 1600, or 1800 ms. The next trial could then either be a cue-target or a cue-only trial, that is an ‘event trial’, or a ‘null trial’ (n = 110) in which there was neither a cue nor a target event. Together with the duration of the null trials, which were of the same duration as the task trials, the interval between two event trials (the interval between the disappearance (offset) of the target in the present trial and the appearance (onset) of the next cue) resulted in 2200 ms on average.

Task conditions and trial types. The present study used a 2 x 2 event-related fMRI design. The first factor was cue type: the cue could be either a rule-cue or a task-cue. The second factor was task transition: the task was either repeated or switched relative to the preceding trial. Based on the instruction cue presented prior to the target, participants were required to distinguish either the color or the gender of the face pictures. If the current task was different from the preceding one, the current trial was classified as a switch trial; if the current task was identical with the previous one, the current trial was classified as a repetition trial. This factor was examined because rule activation (or retrieval) was hypothesized to differ between task repetition trials and switch trials (Mayr & Kliegl 2000; Rogers & Monsell 1995, 2003; Rubinstein et al. 2001). That is, this factor was introduced to examine whether or not preparation for a switched, compared to a repeated, task leads to a modulation of the task rule activation.

Each one of the four conditions (rule / task-cue x task switch / repetition) consisted of 40 cue-only trials and 70 cue-target trials. In sum, there were 440 event trials, the order of which was unpredictable for the participants. In addition, the event trials were randomly intermixed with 110 null trials in which only a black screen was shown. The length of a null trial varied from 2800 ms to 3600 ms, which was similar to the length of the other (task) trials.

For each condition, the cue-related activation can be assessed by measuring the activation on the cue-only trials, whereas target-related activation can be assessed by calculating the contrast between the activation in corresponding cue-target minus cue-only trials.

Stimulus and response conditions. On cue-only trials, only a black screen (i.e., no target) was presented after the presentation of the cue and there was need to respond. On cue-target trials, the target stimulus was a colored face picture. In order to create colored face pictures we merged each one of the original black-white-colored face pictures (2 males and 2 females) with same-sized, faded red rectangles (RGB 187- 124- 106) and yellow rectangles (RGB 179- 155- 111) with Photoshop software. As a result eight colored face pictures were created, which we used as target stimuli: two yellow male faces, two red male faces, two yellow female faces, and two red female faces (with the same face presented in either red or yellow on different trials). Participants were informed by the cue to respond to either the color or the gender of the face. The stimuli (cue and target stimuli) were located on a black background in the centre of the screen and subtanded 5 degrees of visual angle.

Participants used their left and right thumbs for response. They were instructed to respond as fast and as accurately as possible. For half the participants, the S-R mapping rule was male-left, female-right and yellow-left, red-right. This was reversed for the other half: female-left, male-right and red-left, yellow-right.

fMRI measurement

Imaging was performed with a SIEMENS TRIO 3-Tesla scanner at the Beijing MRI Center for Brain Research. T2*-weighted echo-planar images (EPI) with blood oxygenation level-dependent contrast were acquired (TR = 1500 ms, TE = 30 ms, flip angle = 90°, voxel size = 3.4 x 3.4 x 5 mm^3, matrix size = 64 x 64 voxels). Twenty six axial slices (thickness = 4 mm, spacing = 1 mm) were acquired parallel to the AC-PC plane, covering the whole cortex and part of the cerebellum. The order of acquisition of the slices was interleaved. The first five volumes (dummy volumes) were discarded because of possible instabilities in the magnetic field at the beginning of a scan. Stimuli were displayed on a back-projection screen mounted in the bore of the magnet behind the participant's head by using an LCD projector. Participants viewed the screen by wearing mirror glasses.

fMRI data analysis

Preprocessing. Preprocessing of the functional images was carried out using SPM2 (Wellcome Department of Cognitive Neurology, London, UK). Images were interpolated in time (temporal realignment to the middle slice). In addition, they were spatially realigned to the first volume for head movement correction, unwrapped, and then normalized to the standard SPM2 EPI template in MNI space (resampled to 2 x 2 x 2 mm^3 isotropic resolution) with default normalization estimation. The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to account for inter-subject anatomical variability.

Then the image data were modeled by applying a general linear model (Friston et al. 1995). In event-related single-subject analyses, the 4 cue-only and the 4 cue-target conditions were modeled as separate volumes (resulting from the factorial combination of the two cue type (rule-cue vs. task-cue) and the types of task transition (task switch vs. task repetition). Additionally, all error trials were selected to form an error trial volume. The resulting nine volumes were convolved with the hemodynamic response function (HRF), and then beta values of these regressors were estimated according to the ordinary least-squares (OLS) method.

Whole-brain analyses. For group statistics, one-sample t-tests of contrast maps across subjects (random-effects model treating subjects as a random variable) were computed to indicate whether observed differences between conditions were significantly different from zero.

In particular, two main contrasts were calculated: Contrast 1: For cue-only trials, rule-cue minus task-cue trials, intended to isolate extra activation for a rule-cue. Contrast 2: (cue-target trials minus cue-only trials for task-cues) minus (cue-target trials minus cue-only trials for rule-cues), intended to isolate the extra activation related to the target processing when the cue did not specify the rule. In a subsequent conjunction analysis, SPM5 (Nichols et al., 2005) was used to locate the common task rule-related activation between these two main contrasts.

The way in which the remaining statistical contrasts were calculated is detailed in the Results section. Unless stated otherwise, for one-sample t-tests, we used a statistical threshold of $p < 0.001$, uncorrected, covering at least 10 contiguous voxels. We also checked all reported activation foci with a small volume correction procedure (10 mm sphere centred at the voxel with local maximum activation). If not otherwise noted, then the reported foci prove significant at a threshold of $p < 0.05$ (small-volume corrected on both the voxel and the cluster level). For the conjunction analysis, the conjunction hypothesis is "activated in Contrast 1AND Contrast 2", then the conjunction null hypothesis is: (not activated in Contrast 1) OR (not activated in Contrast 2). The statistical threshold was $p < 0.005$, uncorrected, again spanning at least 10 contiguous voxels .

2.3 Results

Behavioral results

Figure 2.1 presents group means of the RTs (left panel) and error rates (right panel) as a function of task transition, for the two types of cue. Mean RTs and error rates were submitted to a 2 x 2 repeated-measures ANOVA with the factors task transition and cue type. RTs were significantly faster in the rule-cue than in the task-cue condition (main effect of cue type, $F(1,12) = 6.71$, $p < 0.05$), which indicates that participants effectively utilized the rule-cue information during the preparation period following cue presentation. The RT advantage for rule-cue compared to the task-cue presentation (i.e., the 'behavioral rule-cue effect') was 17 ms. In addition, RTs were significantly slower for task switch than for task repetition trials (main effect of task transition, $F(1,12) = 12.96$, $p < 0.005$), with switch costs amounting to 25 ms. With mean switch costs of 24 and 27 ms in rule-cue and task-cues conditions, respectively, the interaction effect between cue type and task transition was not significant ($F(1, 12) = 0.114$, $p > 0.7$).

The error rate ANOVA revealed a significant main effect of task transition ($F(1, 12) = 60.91$, $p < 0.0001$): more errors were made on task switch than on task repetition trials. Additionally, a significant interaction between cue type and task transition was obtained ($F(1,12) = 8.84$, $p < 0.05$). Further analyses with separate t-tests revealed elevated error rates in switch compared to repetition trials in the rule-cue and task-cue conditions (both ts (12) > 4.00, both ps < 0.005), and larger switch costs (error rate switch – error rate repetition) in the task-cue (error rate = 6.6 %) compared to the rule-cue condition (error rate = 3.8 %) (t (12) = 2.97, p < 0.05). Thus, as with the RT data, the error data indicated that participants' performance benefited from the presentation of the rule-cue as compared to the task-cue. This benefit was especially pronounced in conditions in which participants had to switch between the tasks as revealed by the increased error rate in the switch compared to the repetition condition.

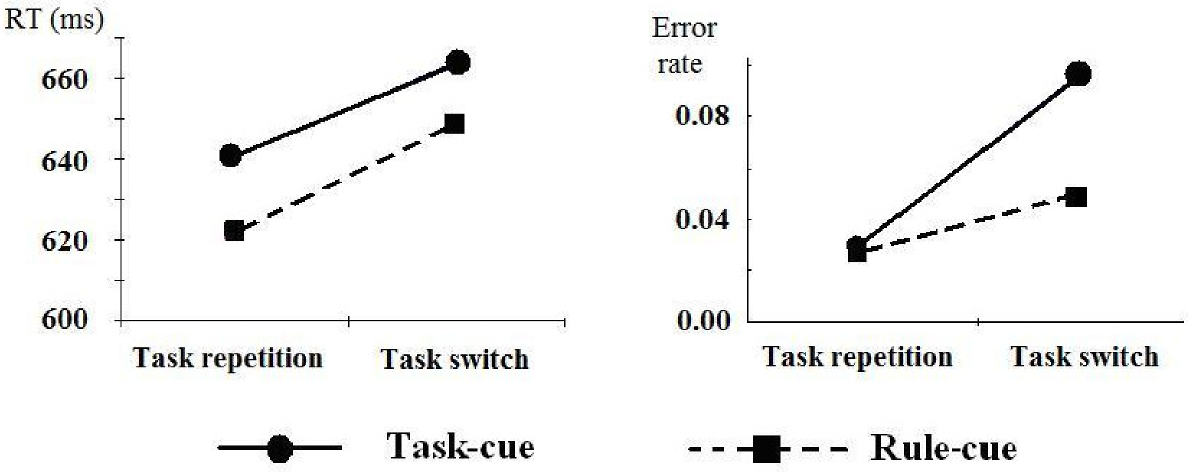


Figure 2.1: Reaction time (RT) and error rates as function of task transition and cue type.

Imaging results

Cue-related activation in rule-cue and task-cue conditions

To identify the cue-related activation, we calculated the main effect for the cue-only trials separately for the rule-cue and task-cue conditions, by fitting the empirical fMRI data to the hemodynamic response function (HRF) described above. The resulting beta values are presented in Figure 2.2. Both the presentation of rule-cues and of task-cues elicited neural activations in a large cortical network, with foci in the MeFC, bilateral regions of the LPFC near the IFJ, and the dorsal and the lateral premotor cortex. Additionally, the medial and lateral parietal lobe, the posterior cingulate cortex (PCC), and the thalamus showed significant activation. Finally, there was bilateral activation in the occipital cortex. In addition to these activation foci which were similar for the two types of cue, two small clusters were activated by the rule-cue in the right and left anterior prefrontal cortex (aPFC). Note that, with a more liberal statistical threshold of $p < .005$, these two clusters also showed activation under task-cue conditions.

In summary, the two types of cue activated highly overlapping brain networks, that is, the preparation processes associated with rule-cues and task-cues are mediated by similar brain regions.

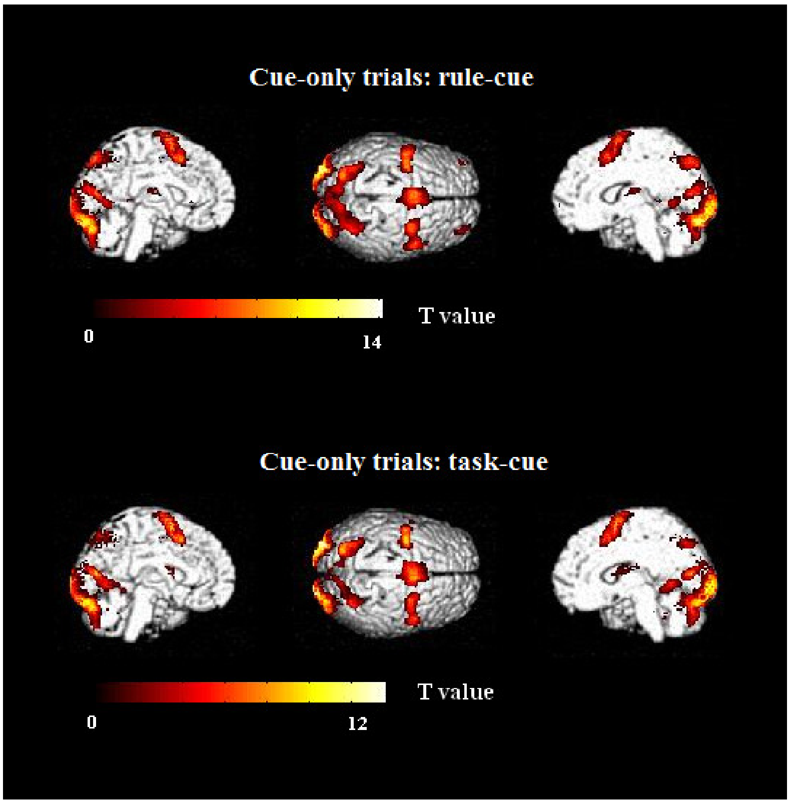


Figure 2.2: Illustration of the brain activation elicited by the presentation of the cue in cue-only trials in the rule-cue condition (top) and in the task-cue condition (below). The resulting cue-related activation across the two cue conditions is associated with the general mechanism of task preparation.

Analysis of rule-related activation during the task preparation and execution periods

As outlined in the Introduction, we expected stronger activation on rule-cue compared to task-cue trials during the preparation period, and, additionally, we assumed these regions to be associated with task rule activation. To examine for this, we calculated a whole-brain contrast of the activation in the rule-cue versus the task-cue condition specifically for cue-only trials. The results of this analysis are presented in Figure 5 and Table 1.

Stronger activation was found for the rule-cue compared to the task-cue condition in the anterior part of the superior frontal gyrus (SFG), that is, the right aPFC, bilaterally in the premotor cortex, and in regions of the MedFC; the latter regions extended from anterior portions in the pre-SMA to posterior portions of the pre-SMA/SMA region. In addition, we found increased activation in the right superior parietal lobe (SPL) and the left precuneus. Finally, activation foci were found bilaterally in the occipital cortex (e.g., in the lingual gyrus and the fusiform gyrus) (see Fig. 2.3a and Table 2.1).

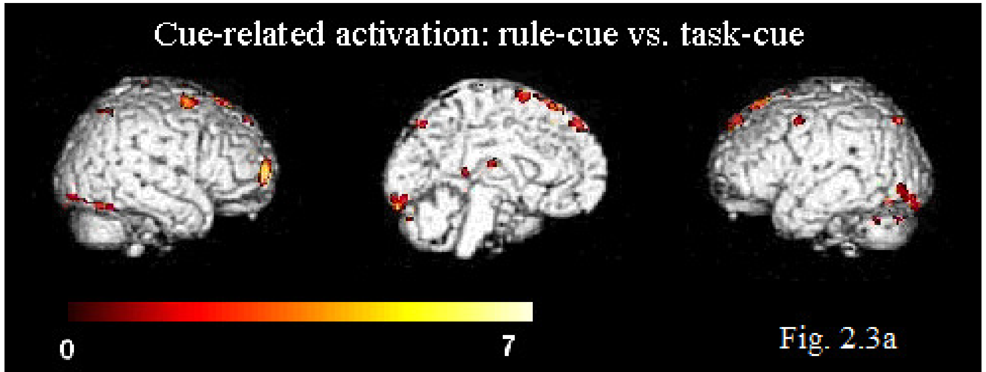
During task execution on cue-target trials, we expected stronger activation in the task-cue, compared to the rule-cue, condition in cortical regions that are associated with the activation of the task rules; this is because of the expected postponement of the rule activation under task-cue conditions. To determine the corresponding activation foci, we contrasted the target-related activation during the execution period in the task-cue and rule-cue conditions. For this purpose, we calculated the contrast: cue-target – cue-only trials separately for the task-cue and rule-cue conditions, so as to derive the corresponding task execution-related activations in both types of trial. Subsequently, we calculated the second-order contrast: task-cue (cue-target minus cue-only trials) – rule-cue (cue-target minus cue-only trials), to compare the target-related activation between the task-cue and rule-cue conditions.

This analysis revealed stronger target-related activity in the task-cue compared to the rule-cue condition in most regions that had proved to be rule-related during the preparation period in the above analysis (see section Cue-related activation). In particular, these regions were the right anterior part of the SFG (aPFC), the right pre-motor cortex, the MeFC (i.e., pre-SMA), the right SPL, and the bilateral lingual and fusiform gyri. In addition to these regions, activity was found in the LPFC, with peak activation in the right posterior MFG that extended into the IFJ (see Fig. 2.3b and Table 2.1).

Subsequently, we performed a conjunction analysis in order to identify the regions commonly associated with task rule activation during the preparation and the execution period (see Fig. 2.3c and Table 2.2). This analysis was calculated across the contrasts rule-cue minus task-cue of the cue-related activation in the preparation period, and task-cue minus rule-cue of the target-related activation in the execution period (see the two analyses above).

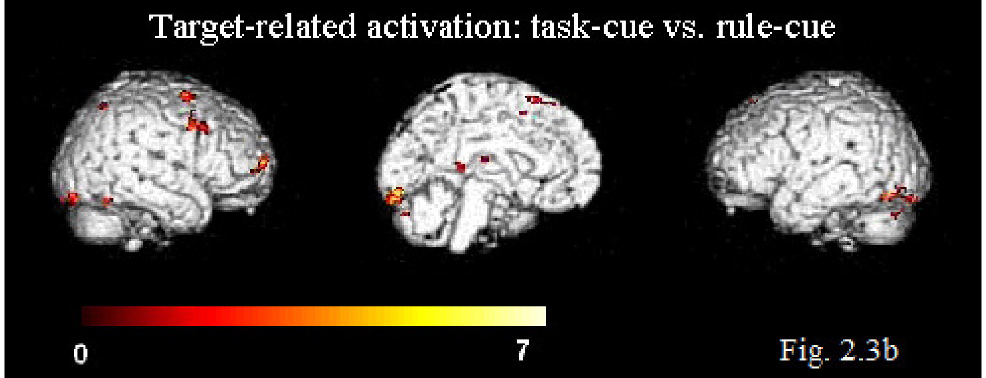
This analysis revealed common activation foci in the right LPFC extending from anterior to posterior portions of the LPFC regions near the IFJ and in anterior and more posterior medial regions of the SFG (pre-SMA/SMA) and the MeFG. Furthermore, the two contrasts exhibited common activity in the right SPL extending into inferior parts of the parietal cortex (IPL), as well as common activation foci in the bilateral lingual gyrus (see Fig. 2.3c and Table 2.2). Note that there are some regions that showed activation in the conjunction analysis but not in both of the two single contrasts ($p < 0.001$, for clusters of ten contiguous voxels); e.g. the right inferior frontal junction (Fig. 2.3a), and the middle part of the dorsolateral prefrontal cortex (Fig. 2.3a and 2.3b). However, these regions showed significant activation foci in the two single contrasts of 2.3a and 2.3b, when using a more liberal threshold of $p < 0.005$.

We propose that these regions, which proved to be activated in the conjunction analysis, are associated with processes of task rule activation either during the preparation period or later, during the execution period subsequent to target presentation.



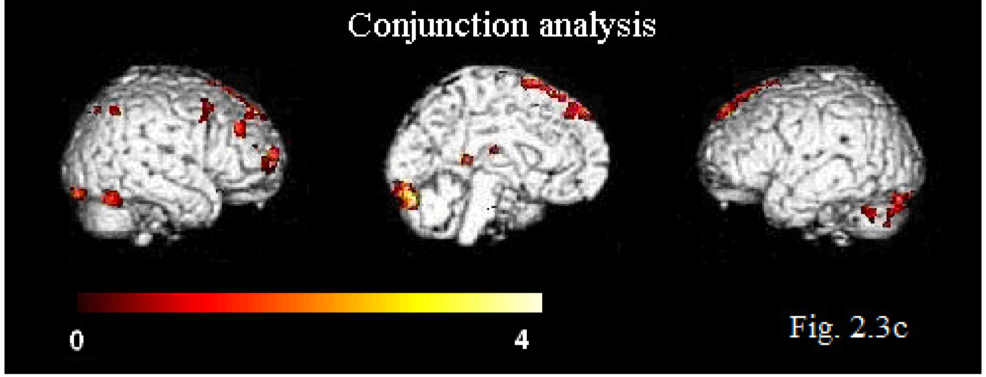
Cue-related activation: rule-cue vs. task-cue

Fig. 2.3a



Target-related activation: task-cue vs. rule-cue

Fig. 2.3b



Conjunction analysis

Fig. 2.3c

Figure 2.3: Cortical activation associated with rule activation in the task-cuing paradigm. Figure 2.3a reveals significant activation in the comparison of rule-cue versus task-cue for cue-only trials. Figure 2.3b reveals brain regions which show increased target-related activation in the comparison of task-cue versus rule-cue trials (for details see text). Note that target-related activation is observed when contrasting activation in cue-target minus cue-only trials. Figure 2.3c represents the brain regions which are observed in the conjunction analysis across the contrasts illustrated in Figure 2.3a and 2.3b. In the conjunction analysis, we used a criterion of $p < 0.005$. Note that there are some regions that showed activation in 5c but not in 2.3a or 2.3b (thresholded with $p < 0.001$, for clusters of ten contiguous voxels); e.g. the right inferior frontal junction (2.3a), and the middle part of the dorsolateral prefrontal cortex (2.3a and 2.3b). However, these regions showed significant activation foci in the single contrasts of 2.3a and 2.3b, when using a more liberal threshold of $p < 0.005$. For further details see Tables 2.1 and 2.2.

Table 2.1. Cortical activation for the comparison of rule-cue versus task-cue in cue-only trials (left) and for the comparison of task-cue versus rule-cue for the target-related activation (right).

Cue-related activation (rule-cue- task-cue)

Region	BA	MNI coordinates	Voxel number	T max
R anterior SFG	10	38, 62, 6	186	6.15
R MFG	6	38, 2, 62	97	7.56
L MFG/precentral gyrus	6	-48, 2, 48	23	4.66
MeFG	8	0, 50, 48	62	6.08
Medial SFG (Pre-SMA)	6	0, 34, 60	100	6.91
Medial SFG (Pre-SMA/SMA)	6	-2, 8, 72	67	5.41
R SPL	7	38, -58, 56	17	3.98
L Precuneus	7	-18, -76, 48	62	6.09
L Fusiform Gyrus/MOG	19	-44, -72, -20	49	4.88
R Fusiform Gyrus	37	48, -52, -24	16	4.04
L MOG/IOG	19, 18	-44, -84, -12	69	5.00
L Lingual Gyrus/ Fusiform Gyrus	17, 18	-6, -92, -16	91	5.34
R Lingual Gyrus	18	6, -86, -16	32	4.91

Target-related activation (task-cue- rule-cue)

Region	BA	MNI coordinates	Voxel number	T max
R anterior SFG	10	36, 64, 8	67	5.36
R MFG	6	38, 4, 64	43	7.34
R MFG	9, 8	56, 18, 38	97	5.13
Medial SFG (Pre-SMA)	6	0, 18, 62	43	4.83
MeFG(Pre-SMA)	6	-2, 12, 50	14	4.30
R SPL	7	36, -62, 56	11	4.04
L Fusiform Gyrus /MOG, IOG	19	-42, -68, -16	91	4.82
R Fusiform Gyrus	37, 20	54, -58, -20	17	4.50
L/R Lingual Gyrus /Fusiform Gyrus	18, 19	-8, -92, -18	198	5.23

R Fusiform Gyrus/ MOG/IOG	19, 18	40, -66, -20	57	4.84	R Fusiform Gyrus, MOG /Lingual Gyrus	18, 19	26, -84, -14	55	4.86

Note: SFG = superior frontal gyrus; MFG = middle frontal gyrus; MeFG = medial frontal gyrus; SMA = supplementary motor area;

SPL = superior parietal lobe; IPL = inferior parietal lobe; MOG = middle occipital gyrus; IOG = inferior occipital gyrus.

Target-related activation is observed when contrasting activation in cue-target and cue-only trials (see text).

Table 2.2. Significant activity in the conjunction analysis across the contrast rule-cue versus task-cue (cue-only trials) and the contrast task-cue versus rule-cue (target-related activation), ($p < 0.005$).

Region	**BA**	**MNI coordinates**	**Voxel number**	**T max**
R MFG/SFG	10	32, 64, 14	137	3.69 **
R MFG/SFG	46, 9	48, 38, 32	90	3.47 **
R MFG	8, 6	50, 8, 40	64	2.90
Medial SFG/ MeFG (pre-SMA)	8, 6	0, 36, 58	413	3.71 **
R Inferior Parietal Lobule	40	52, -58, 46	40	2.94
R Superior Parietal Lobule	7	38, -74, 48	23	2.95
L Lingual Gyrus/ Fusiform Gyrus	18	-8, -92, -18	157	3.55 **
R Lingual Gyrus/ Fusiform Gyrus	18	12, -92, -18	110	3.74 **

Note: SFG = superior frontal gyrus; MFG = middle frontal gyrus; MeFG = medial frontal gyrus; pre-SMA = supplementary motor area. Regions marked by ** showed significant activation at a lower threshold of $p < .001$, uncorrected.

Neural activation in the preparation period and the need to prepare for a switch

Although the aim of the present study was to understand the neural correlates of task rule activation, the adopted paradigm allows us also to investigate the processes genuine to task-switching situations in which participants alternate between different task rules. Therefore, we also examined whether the rule activation in the preparation period is modulated by the need to prepare for a task switch, compared to a repetition. For this analysis, the switch-related activity on cue-only trials (collapsed across cue types) was examined by calculating the contrast: cue-only (switch – repetition). This contrast revealed cortical activation to be increased only in the medial SFG (pre-SMA) for the preparation for a task switch versus a repetition, as is illustrated in Figure 2.4. In an additional ROI analysis, we aimed to test whether the need to process a rule-cue or a task-cue leads to any additional modulations of the neural activity in this switch-related region during the preparation period. In order to decrease the second-order error of overlooking a possible modulation effect of the switch-related activity, we selected an ROI that depended on the particular switch-repetition contrast; according to Kriegeskorte et al. (2009), this way of ROI selection increases the probability to find any effects related to the depending contrast (i.e., in the present case, the switch-repetition contrast). In more detail, we defined an ROI consisting of eleven active voxels surrounding the local-peak voxel in the contrast: cue-only (switch – repetition), and for this ROI, we extracted the β-values individually for each participant in the rule-cue and task-cue conditions dependent on the task transition (switch vs. repetition). The data are presented in Figure 6. A 2 x 2 repeated-measures ANOVA of the β-values revealed significant main effects of the factors task transition ($F(1,13) = 5.075$, $p < 0.05$) and cue type ($F(1,13) = 17.820$, $p < 0.001$), but no significant interaction ($F(1,13) < 1$). The non-significance of the interaction means that the need to prepare for a task switch (compared to a less demanding task repetition) affects the activation in the medial SFG on cue-only trials to the same degree in the rule-cue and the task-cue condition. In other words, the need to process a rule-cue or a task-cue does not modulate the switch-related activation in the medial SFG during the preparation period.

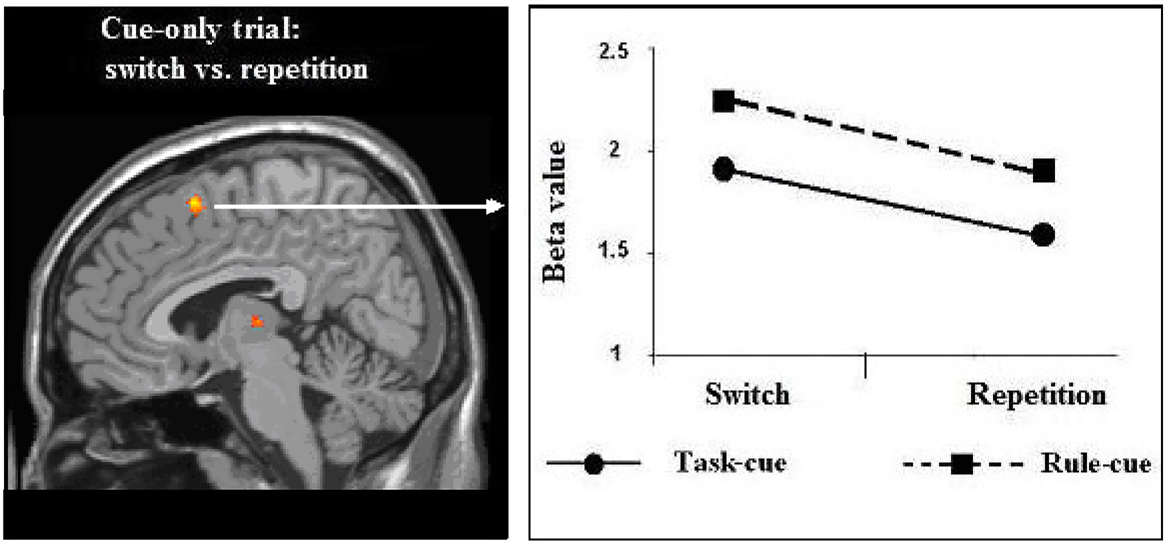


Figure 2.4: Illustration of switch-related activation in cue-only trials. The activation in medial parts of the superior frontal gyrus (SFG; MNI coordinates -8, 14, 58) was found by comparing the activation in switch and repetition trials independently on the cue type, i.e. rule-cue and task-cue. β-values in the switch-related region-of-interest (ROI) in the medial SFG as a function of cue type and task transition (cue-only trials) are presented in the right side. For details about the ANOVA results on the β-values see text.

2.4 Summary of results

The present paradigm permits task rule-related brain regions to be identified by analyzing the effects of rule-cues and task-cues on brain activity separately for the preparation and execution periods of the task. In the preparation period, rule activation related regions should be activated more strongly following the presentation of rule-cues as compared to task-cues. Conversely, for the execution period, rule-related activation would be expected specifically upon target presentation if task rules were not activated sufficiently during the preparation period; this pattern should be revealed by the contrast of the target-related activation in the task-cue compared to the rule-cue condition. In line with these predictions, the conjunction analysis revealed similar frontoparietal networks of activation foci in the corresponding contrasts, that is: the contrast of rule-cue minus task-cue for cue-only trials (preparation period) and the contrast comparing target-related activation on task-cue versus rule-cue trials (execution period). The common activation foci in these two contrasts included the anterior and middle parts of the right MFG and SFG, the posterior region of the MFG near the IFJ, regions in the medial SFG extending from anterior to posterior portions of the pre-SMA, as well as the right SPL and IPL. All these activations conformed to the pattern expected for cortical regions that are correlated with the mechanisms underlying task rule activation.

CHAPTER 3

fMRI Experiment 2

3.1 Research hypothesis and expectations

This experiment tried to find the evidence for the hypothesis that the preparatory attentional control can bias sensory processing via amplifying the activity of the task - relevant stimuls-specific brain region.

The preparatory modulation was expected in the posterior stimuls-specific brain regions (i.e., face specific and number specific regions). In particular, significant additional activity comparing to null trials was expected to be found in the preparation period of face task in right FFA; while in the preparation period of number task, significant additional activity comparing to null trials was expected to be found in right IPSnum.

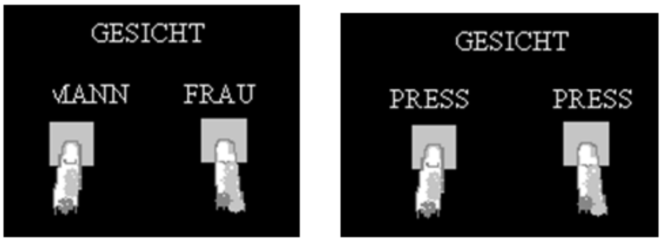
3.2 Methods

Subjects

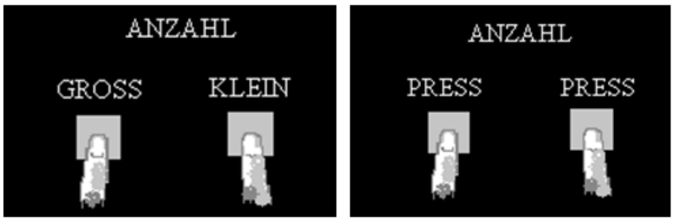
Fourteen healthy right-handed volunteers with normal or corrected to normal vision participated in the experiment (six males, ages 19-33, mean age: 24.9, SDV: 4.4) after obtaining informed consent according to the Declaration of Helsinki. Each participant was paid 20 €. Two participant's data were excluded from the following analysis because of high error rate (more than 20 %). Thus, ultimately, 12 participants' data sets were available for analysis (six male, ages 19-33, mean age: 24.4, SDV: 4.6).

Experiment setting for the main task

Paradigm and procedure. The task to be performed by the participants was either gender discrimination (female or male) or number discrimination (bigger or smaller than five, it is called big or small for short). Each trial began with the presentation of a cue for a fixed duration of 1200 ms, which could either be a rule-cue or a task-cue (Fig. 3.1). Both cues displayed an instruction for the upcoming task; however, a precise instruction about the required task rule was provided only in the rule-cue condition (Fig. 3.1, upper panel). On cue-only trials (n = 200 trials, of which 50 presented a rule-cue and 50 a task-cue for face task, and the same amount for number task), there was no target following the cue offset, but only a black screen that lasted for 600 ms, and there was no need for participants to make a response (Fig. 3.2, right panel).



rule cue



task cue

Figure 3.1: Illustration of the rule-cue and task-cue displays. In the rule-cue and the task-cue conditions, the current task was indicated by the words "ANZAHL" (number) and "GESICHT" (face), respectively. In the rule-cue condition (upper row), additional information indicated the assignments of the response keys to the stimulus categories male and female in the gender task and big and small in the number task.

In contrast, on cue-target trials (n = 280, of which 70 presented a rule-cue and 70 a task-cue for face task, and the same amount for number task), the cue was followed by picture contains both face and number that was presented for 600 ms (Fig. 3.2). Participants were to respond to either the number or the face depicted in the target display, depending on the instruction of cue. Participants made two-alternative forced-choice responses using either their left or right finger, with response sets counterbalanced across participants. After the offset of the target picture, a black screen was presented for a variable interval of 1800, 2500, 3100, 3900, or 4600 ms. The next trial could then either be a cue-target or a cue-only trial, that is an 'event trial', or a 'null trial' (n = 140) in which there was neither a cue nor a target event.

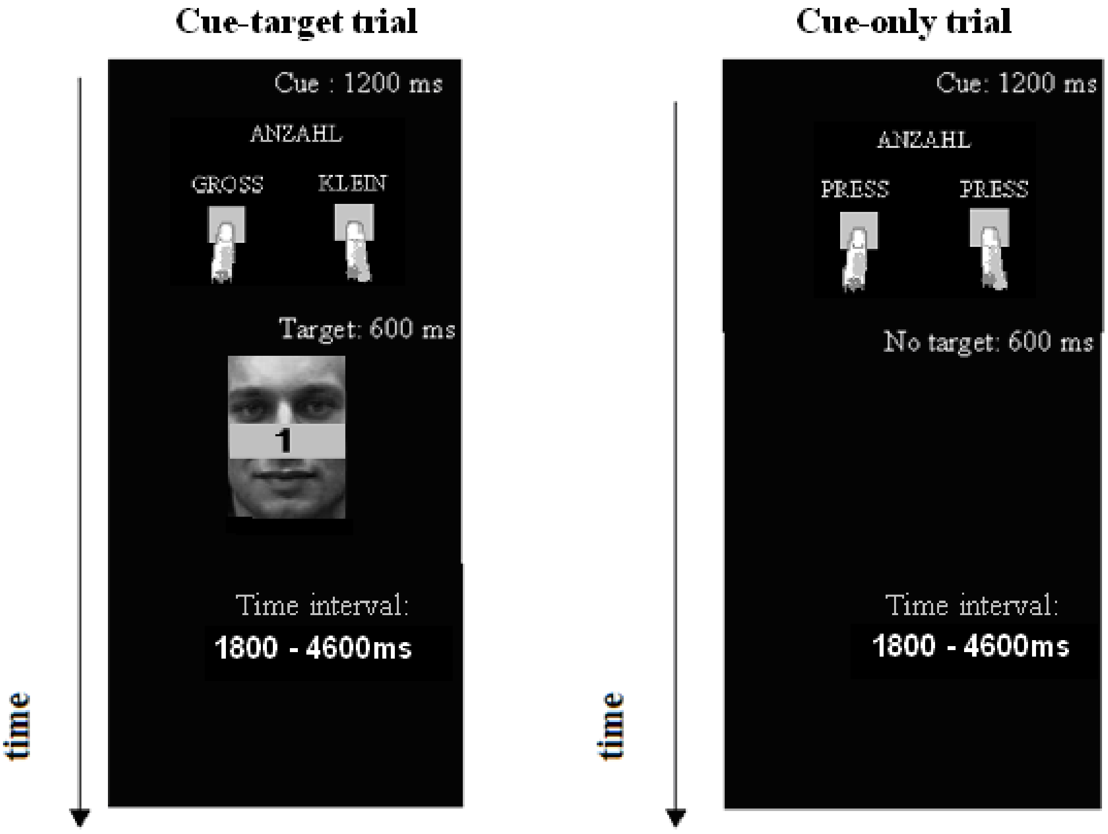


Figure 3.2: Procedure of Experiment 2

Task conditions and trial types. The present study used a 2 x 2 x 2 event-related fMRI design. Similar to the fMRI Experiment 1, the two factors: cue type (rule-cue or task-cue) and task transition (task switch and repetition) were involved. Another factor is task type: the task could either be a number or face task.

Each one of the eight conditions (rule / task-cue x task switch / repetition) consisted of 25 cue-only trials and 35 cue-target trials. In sum, there were 480 event trials, the order of which was unpredictable for the participants. In addition, the event trials were randomly intermixed with 140 null trials in which only a black screen was shown. All the trials were assigned into four runs lasting 12 min 40s each. The participant had short break of one or two minutes between two runs. At the beginning of each run, a word "Attention" was presented for 2 seconds to remind the participants to back to the task performing.

For each condition, the cue-related activation can be assessed by measuring the activation on the cue-only trials, whereas target-related activation can be assessed by calculating the contrast between the activation in corresponding cue-target minus cue-only trials.

Stimulus and response conditions. On cue-only trials, only a black screen (i.e., no target) was presented after the presentation of the cue and there was need to respond. On cue-target trials, the target stimulus was a face picture with a word of number locating in the region of nose. Two males and two females' pictures were used, the number could be "EINS" (one), "ZWEI"(two), "ACHT" (eight) or "NEUN"(nine). As a result 16 face-and-number pictures were used as target stimuli. Participants were informed by the cue to respond to either the face or the number. The stimuli (cue stimuli and target stimuli) were located on a black background in the centre of the screen and subtanded 5 degrees of visual angle.

Participants used their left and right finger for response. They were instructed to respond as fast and as accurately as possible. For half the participants, the S-R mapping rule was male-left, female-right and big-left, small-right. This was reversed for the other half: female-left, male-right and small-left, big-right.

fMRI measurement

Imaging was performed with a SIEMENS TRIO 3-Tesla scanner at the Klinikum Großhadern (Institute for Clinical Radiology), Ludwig-Maximilians-Universität in Munich. T2*-weighted echo-planar images (EPI) with blood oxygenation level-dependent contrast were acquired (TR = 1500 ms, TE = 30 ms, flip angle = 80°, matrix size = 64 x 64 voxels). Twenty three axial slices (thickness = 4 mm, spacing = 1 mm) were acquired parallel to the

AC-PC plane, covering the whole cortex. The order of acquisition of the slices was interleaved. The first four volumes (dummy volumes) were discarded because of possible instabilities in the magnetic field at the beginning of a scan. Stimuli were displayed on a back-projection screen mounted in the bore of the magnet behind the participant's head by using an LCD projector. Participants viewed the screen by wearing mirror glasses.

fMRI data analysis

Preprocessing of the functional images was carried out using SPM5 (Wellcome Department of Cognitive Neurology, London, UK). Images were interpolated in time (temporal realignment to the middle slice). In addition, they were spatially realigned to the first volume for head movement correction, unwrapped, and then normalized into MNI space (resampled to 2 x 2 x 2 mm^3 isotropic resolution) with default normalization estimation. The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to account for inter-subject anatomical variability.

Then the image data were modeled by applying a general linear model (Friston et al. 1995). In event-related single-subject analyses, the 8 cue-only and the 8 cue-target conditions were modeled as separate volumes (resulting from the factorial combination of the two task types (face vs. number), two cue types (rule-cue vs. task-cue) and the types of task transition (task switch vs. task repetition). Additionally, the introduction which occurred at the beginning of each run, the null trials, and all error trials were separately selected to form three event volume. The resulting 19 volumes were convolved with the hemodynamic response function (HRF), and then beta values of these regressors were estimated according to the ordinary least-squares (OLS) method. The beta values of the cue-only trials were the activation parameters analyzed in the ROI analysis, while the beta values for the cue-target trials subtracted the beta values for their corresponding cue-only trials resulted the activation parameters for target period activation, which were analyzed in the ROI analysis.

Another general linear model was built in order to replicate the findings of fMRI Experiment 1. Similar to the fMRI Experiment 1, the 4 cue-only and the 4 cue-target conditions were modeled as separate volumes (resulting from the factorial combination of the two cue type (rule-cue vs. task-cue) and the types of task transition (task switch vs. task repetition). The introduction which occurred at the beginning of each run, the null trials, and all error trials were selected to form an event volume additionally. The resulting 11 volumes were convolved with the hemodynamic response function (HRF), and then beta values of these regressors were estimated according to the ordinary least-squares (OLS) method. The for the whole brain analyses, similar conjunction analysis was performed to locate the common task rule-related activation between these two main contrasts: Contrast 1: For cue-only trials, rule-cue minus task-cue trials (use the threshold of $p < 0.001$); Contrast 2: (cue-target trials minus cue-only trials for task-cues) minus (cue-target trials minus cue-only trials for rule-cues) (use the threshold of $p < 0.001$). For the conjunction analysis, the statistical threshold was $p < 0.005$, uncorrected.

Experiment design for the localization task

After the main experiment, participants performed one run of localizer tasks to determine the individual Regions of Interest (ROIs) in the FFA and IPSnum relevant for face processing and number processing respectively.

Paradigm and procedure.

In this localization task the participants respond to picture containing either only face or only number alternatively without the giving of cue.

Participants performed 18 alternating task blocks to localize the FFA and the IPSnum, respectively. Each block consisted of 8 trials with trial duration of 2 seconds. Stimulus duration was 600 ms; it was identical to that in the main experiment. In the face blocks, participants performed the face component task of the main experiment and in the number blocks, participants performed the number component task of the main experiment, using the same response rules of main experiment. Four face pictures (2 female and 2 male) and four words of number (“EINS”; “ZWEI”; “ACHT” “NEUN”) which appeared in the main task were used, but this time no confound picture (face-and-number picture) but only the relevant stimuli were presented in the respective blocks.

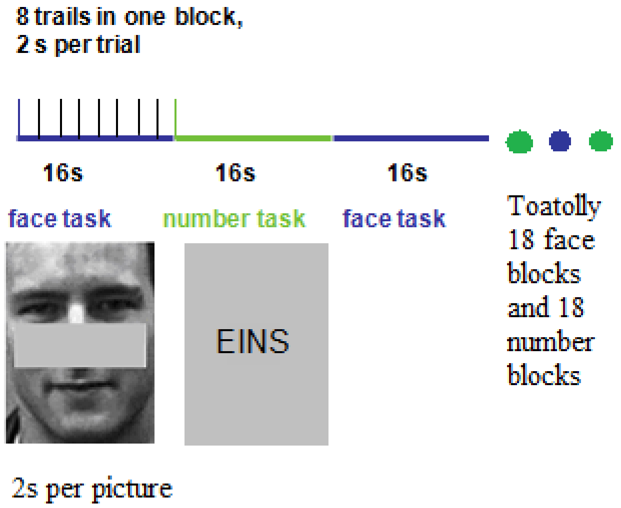


Figure 3.3: Procedure of the localization task.

fMRI measurement

The localization task was performed one minute after the main task four runs, with the same fMRI measurement setting.

fMRI data analysis

Preprocessing. Preprocessing of the functional images was carried out using SPM5 (Wellcome Department of Cognitive Neurology, London, UK). Images were spatially realigned to the first volume for head movement correction, unwrapped, and then normalized into MNI space (resampled to 2 x 2 x 2 mm^3 isotropic resolution) with default normalization estimation. The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to account for inter-subject anatomical variability.

Then the image data were modeled by applying a general linear model (Friston et al. 1995). In event-related single-subject analyses, the face task and number task conditions were modeled as separate volumes. Additionally, all error trials were selected to form an event volume. The resulting three volumes were convolved with the hemodynamic response function (HRF), and then beta values of these regressors were estimated according to the ordinary least-squares (OLS) method.

Whole-brain analyses. For group statistics, one-sample t-tests of contrast maps across subjects (random-effects model treating subjects as a random variable) were computed to indicate whether observed differences between conditions were significantly different from zero. A statistical threshold of $p < 0.001$, uncorrected, was used, covering at least 10 contiguous voxels.

The contrast of ‘face – number’ and the reversed one ‘number – face’ were calculated to find the group activity peaks in FFA and IPSnum respectively, started from which, I then found individual face specific and number specific regions.

Region-of-Interest (ROI) Analyses. For the FFA and the IPSnum these ROIs were determined in every participant. The FFA and the IPSnumber activity for the contrasts 'face-number' and 'number-face' were used for every participant. The statistical threshold used was p < 0.01, uncorrected, covering at least 10 contiguous voxels.

Starting from the location of the group activity peak in the localization task, the nearest peak per participant was determined as centre of the individual cube ROI mask (6mm side length). From the voxels covered by these masks we extracted the parameter estimates from the time series of every individual participant for all 16 task conditions (produced by the beta values, see fMRI experiment2 _ *fMRI data analysis*). The 8 activation parameters of cue period occupied most interesting. They were compared by ANOVA with the factors task type (face vs. number), cue type (rule-cue vs. task-cue) and task transition (task switch vs. task repetition). The 8 parameters of cue-target trails subtracted the corresponding cue-only trails parameters to obtain the parameters for target period activation, which then were compared by ANOVA with the factors task type, cue type and task transition also.

3.3 Results

Behavioral Results

Mean reaction time were submitted to a 2 x 2 x 2 repeated-measures ANOVA with the factors of task type (face or number), cue type (rule-cue or task-cue) and task transition (task switch or repetition) (see Fig 3.4).

No significant effect was found for the main effect of task type (F(1,11) = 0.82, p =0.38). The task difficulties of these two tasks are balanced.

RTs were significantly faster in the rule-cue than in the task-cue condition (main effect of cue type, $F(1,11) = 4.84$, $p < 0.05$), which indicates that participants effectively utilized the rule-cue information during the preparation period following cue presentation. The RT advantage for rule-cue compared to the task-cue presentation (i.e., the ‘behavioral rule-cue effect’) was 22 ms.

In addition, RTs were significantly slower for task switch than for task repetition trials (main effect of task transition, $F(1,11) = 7.67$, $p < 0.05$), with switch costs amounting to 14 ms.

With mean switch costs of 1 and 27 ms in rule-cue and task-cues conditions, respectively, the interaction effect between cue type and task transition tends to be significant ($F(1,11) = 3.61$, $p = 0.08$). Further analyses with separate t-tests revealed switch cost only exist in the task-cue condition ($t(11) = 2.74$, $p < 0.01$) but not in the rule-cue condition ($t(11) = 0.1$, $p = 0.46$). This may indicate that the rule-cue information could be helpful for the conquering of switch cost.

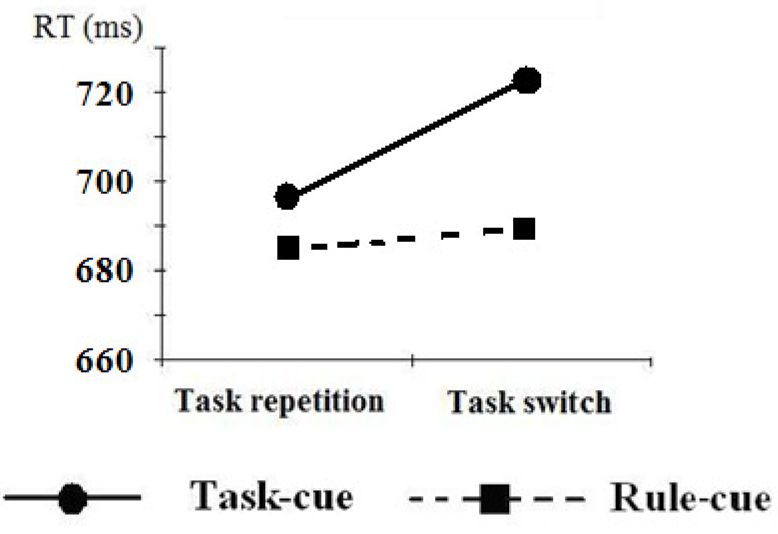


Figure 3.4: RT as function of task transition and cue type

Error rates were submitted to a 2 x 2 x 2 repeated-measures ANOVA with the factors task type, cue type and task transition.

No significant effect was found for the main effect of task type (F (1, 11) = 0.74, p =0.41), neither no significant effect for the main effect of task transition either (F (1, 11) = 2.00, p = 0.19).

Error rates were significantly reduced in the rule-cue than task-cue condition (3.5% vs. 5.1%; main effect of cue type: F (1, 11) = 9.81, $p < 0.01$), which indicates that participants effectively utilized the rule-cue information during the preparation period following cue presentation.

With mean rule-cue benefit of 3% and 0.2% in face task and number task conditions respectively, the interaction effect between task type and cue type was significant (F(1,11) = 9.30, $p < 0.05$). Further analyses with separate t-tests revealed significant rule-cue benefit in the face task condition (t(11) = 4.94, $p < 0.0001$) but not in the number task condition (t(11) = 0.29, p = 0.78). It indicated that participants utilized the rule-cue information more effectively in the preparation of the face task than the number task.

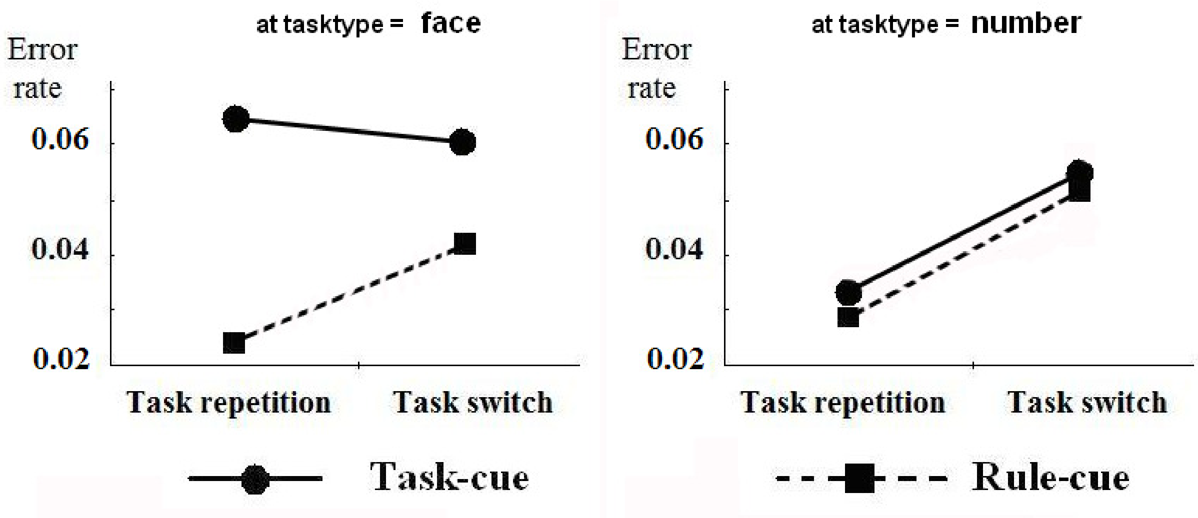


Figure 3.5: Error rates as function of task transition and cue type in face and number task

Image Results

This experiment was mainly designed to find the preparatory attentional bias in the posterior brain regions. But before reporting the activation of the posterior ROIs, the replication of findings in Experiment 1 will briefly be introduced.

The replication of findings in Experiment 1

Similarly as in Experiment 1, I adopted the task-cuing paradigm and cue-only trial design in Experiment 2, which allowed me to test for the replicability of the findings of Experiment 1.

The general task preparation brain network

To identify brain network for general task preparation, the activation in cue-only trials was compared to the null trials separately for the rule-cue and task-cue conditions, highly consisted with the finding in Experiment 1, a large frontal-paratial network, including foci in the MeFC, bilateral LPFC near the IFJ, the dorsal and the lateral premotor cortex and the medial and lateral parietal lobe, were elicited by the rule-cues and task-cues (Fig. 3.6).

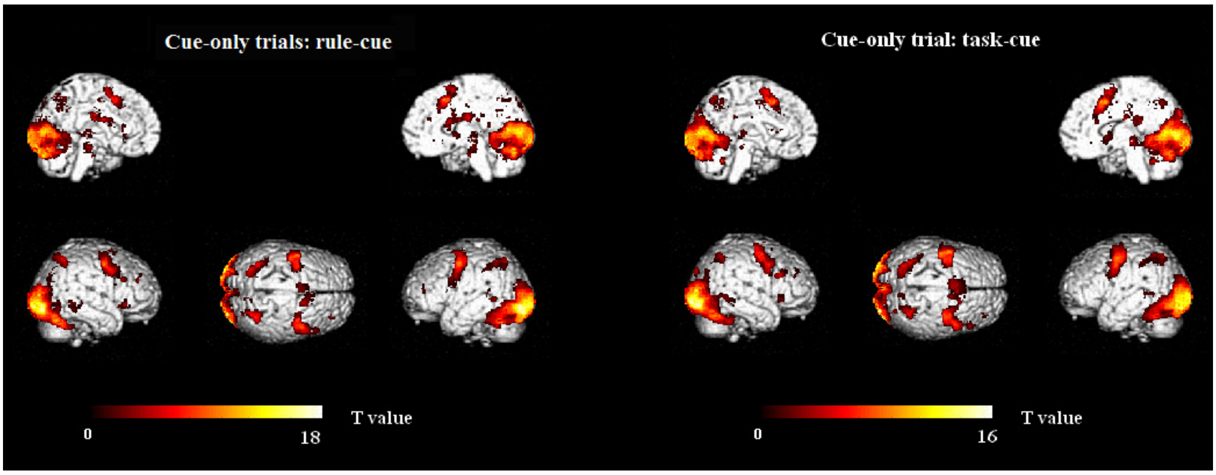


Figure 3.6: Brain network for general task preparation elicited by rule-cues and task-cues

The foci of rule implementation

Similar to the fMRI experiment1, a conjunction analysis was performed in order to reveal the rule-related neural activity in fMRI Experiment 2.

This analysis was calculated across the contrasts rule-cue minus task-cue of the cue-related activation in the preparation period, and task-cue minus rule-cue of the target-related activation in the execution period. Several rule-related foci in Experiment 1 again showed activity in the present conjunction analysis, the foci located in the medial PFC, right IFJ and aPFC (Fig. 3.7). They are associated with processes of task rule activation either during the preparation period or later, during the execution period subsequent to target presentation.

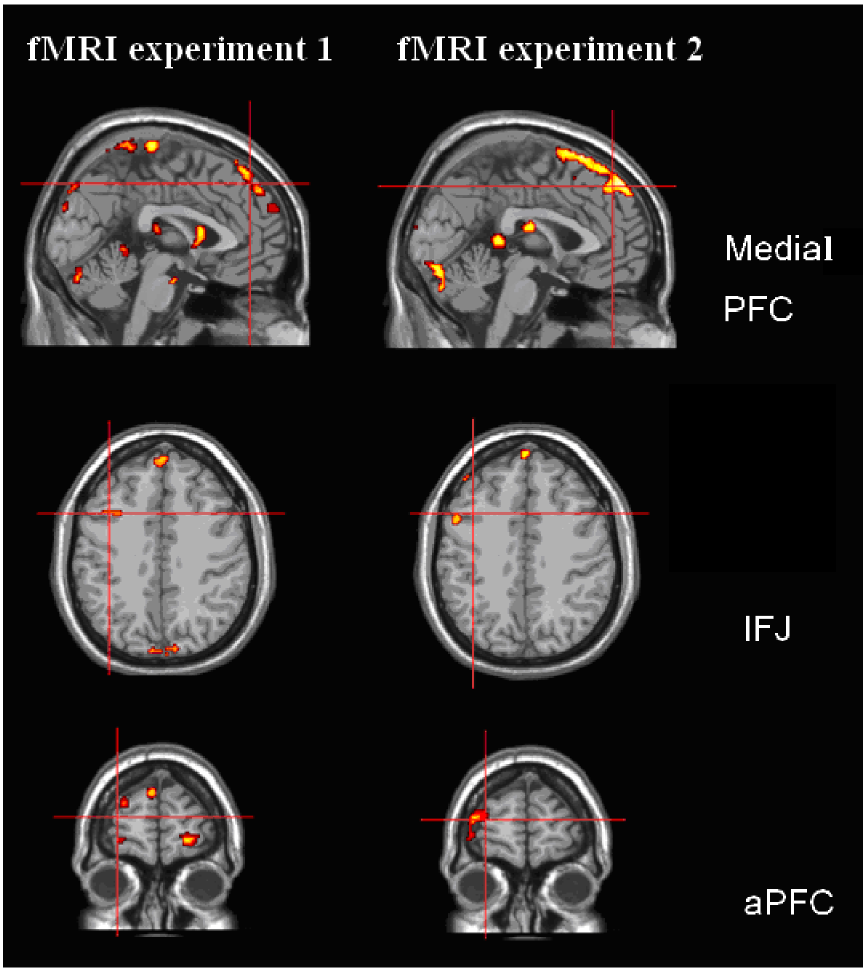


Figure 3.7: Foci of rule implementation activated in both fMRI Experiment 1 and 2

The switch specific preparatory activity in pre-SMA

A higher activation for the preparation of a switched task than repeated task was found in the left medial frontal gyrus, the left cingulate gyrus near medial SFG, as well as the left inferior parietal lobule, right superior temporal gyrus and right extra-nuclear. The activation in the left cingulate gyrus and medial frontal gyrus are close to the medial SFG, which showed switch-additional activity for the same contrast in Experiment 1.

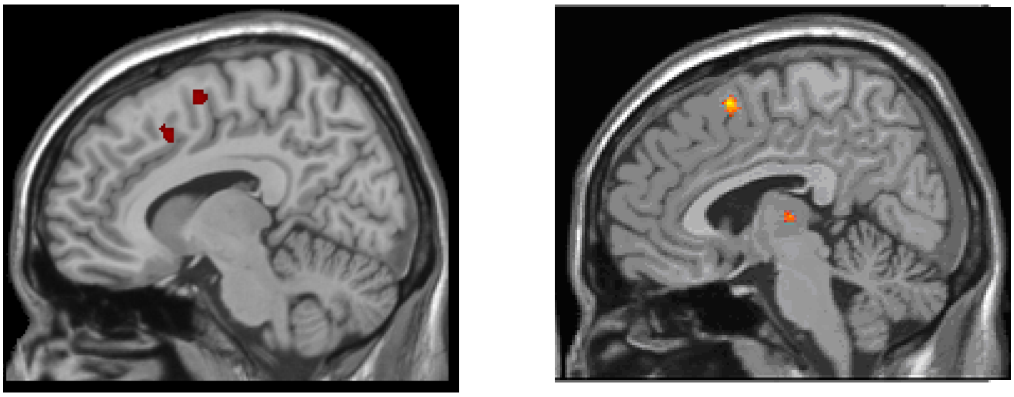


Figure 3.8: Illustration of switch-related activation in cue-only trials.
In Experiment 2 (left), the activation was found near the medial SFG (MNI coordinates: -10, 14, 44) and in the medial frontal gyrus (MNI coordinates: -8, 0, 60). In Experiment 1(right), activation was found in the medial SFG (MNI coordinates: -8, 14, 58)

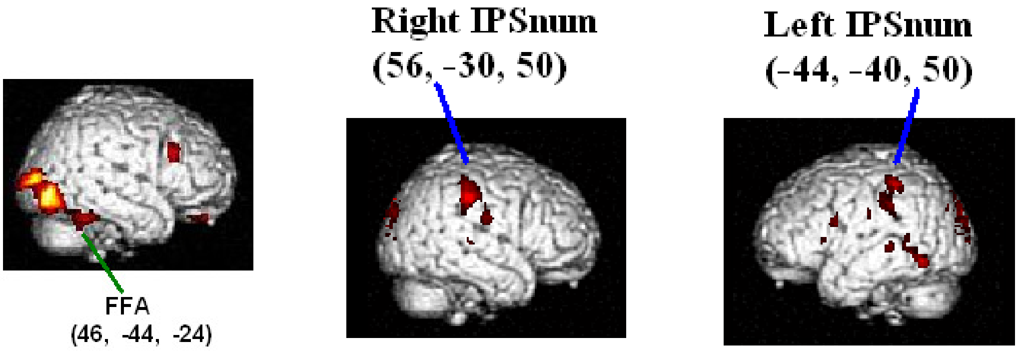
Regions of interest (ROIs) analysis

For the main aim of Experiment 2, I conducted an ROI analysis in order to find the preparatory attentional modulation in the posterior brain regions.

Group activity peaks for face and number stimulus processing

In order to find the group peak in the face specific region and number specific region, the contrasts of ‘face - number’ and ‘number - face’ for the localization tasks were calculated.

Note that these are not the only regions involved in the processing of face and number (see Fig. 3.9). However, the FFA (typically the right side) and bilateral IPSnum have been shown to be consistently involved in the processing of face and number categories in numerous studies (Kanwisher et al. 1997, 1999; Chochon et al. 1999; Dehaene et al. 2003) and were therefore used as representative regions for the processing of these stimulus categories in the present study. Note that the right FFA was more sensitive to the face processing than the left FFA, therefore, for the following identification of individual face specific ROIs, the right FFA should be considered first. If the participants showed no significant activity near the right FFA (with the threshold of $p < 0.05$, unc), then the left FFA would be considered. On other hand, the IPSnum is critical for number processing (Dehaene et al., 2003), while the right side is especially sensitive to the number comparison task (Chochon et al., 1999) which fits the present number task well. Therefore, for the following identification of individual number specific ROIs, the right IPSnum was considered first. If the participants showed no significant activity near the right IPSnum (with the threshold of $p < 0.05$, unc), then the left IPSnum would be considered.



Contrast: face - number

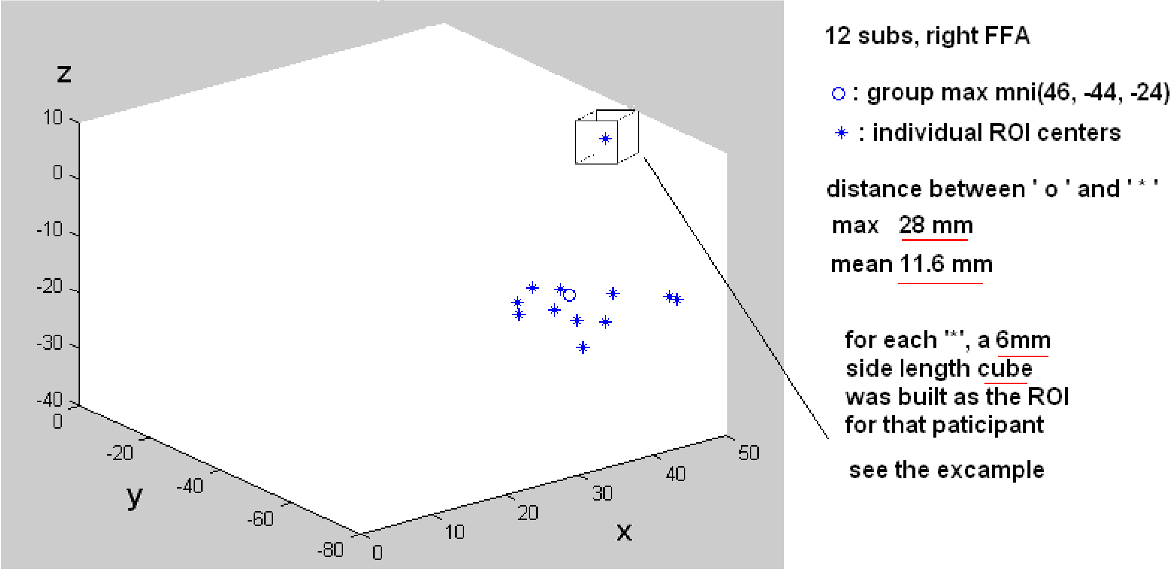
Contrast: number – face

Figure 3.9: FFA and IPSnum activation and their peak

Identification of the individual ROIs

The face specific ROIs

All the participants showed significant larger activation in the contrast of 'face - number' near the group peak in the right FFA (MNI (46,-44,-24)). The nearest peak (individual) was found for each participant. Than all the activation voxels within a 6 mm-side length cube mask were selected as the corresponding participant's face specific ROI (see Fig. 3.10).



12 subs, right FFA

o : group max mni(46, -44, -24)

* : individual ROI centers

distance between ' o ' and ' * '
max 28 mm
mean 11.6 mm

for each "*", a 6mm
side length cube
was built as the ROI
for that paticipant

see the excample

Figure 3.10: The face specific ROIs for twelve participants (in the right FFA).

The number specific ROIs

Eleven of the twelve participants showed significant larger activation in the contrast of 'number - face' near the group peak in the right IPSnum (MNI (56,-30,50)), and the nearest peak (individual) was found for each of these eleven participants. Than all the activation voxels within the 6mm-side length cube mask were selected as the corresponding participant's number specific ROI (see Fig. 3.11).

The remaining participant showed no significant larger activation in the contrast of ‘number - face’ near the group peak in the right IPSnum (no IPS activation even at the threshold of $p < 0.05$ within 30 mm range from the group max in right IPSnum); however, a significant larger activation was found for this participant in the left IPSnum (‘number - face’, $p < 0.01$, unc). Therefore, the nearest peak (individual) to the left IPSnum peak (MNI (-44,-40,50) was idientified as the number specific region (14 mm distance to the group peak in left IPSnum) for that participant; here all activated voxels within the 6 mm-side length cube mask were selected as the corresponding participant’s number specific ROI.

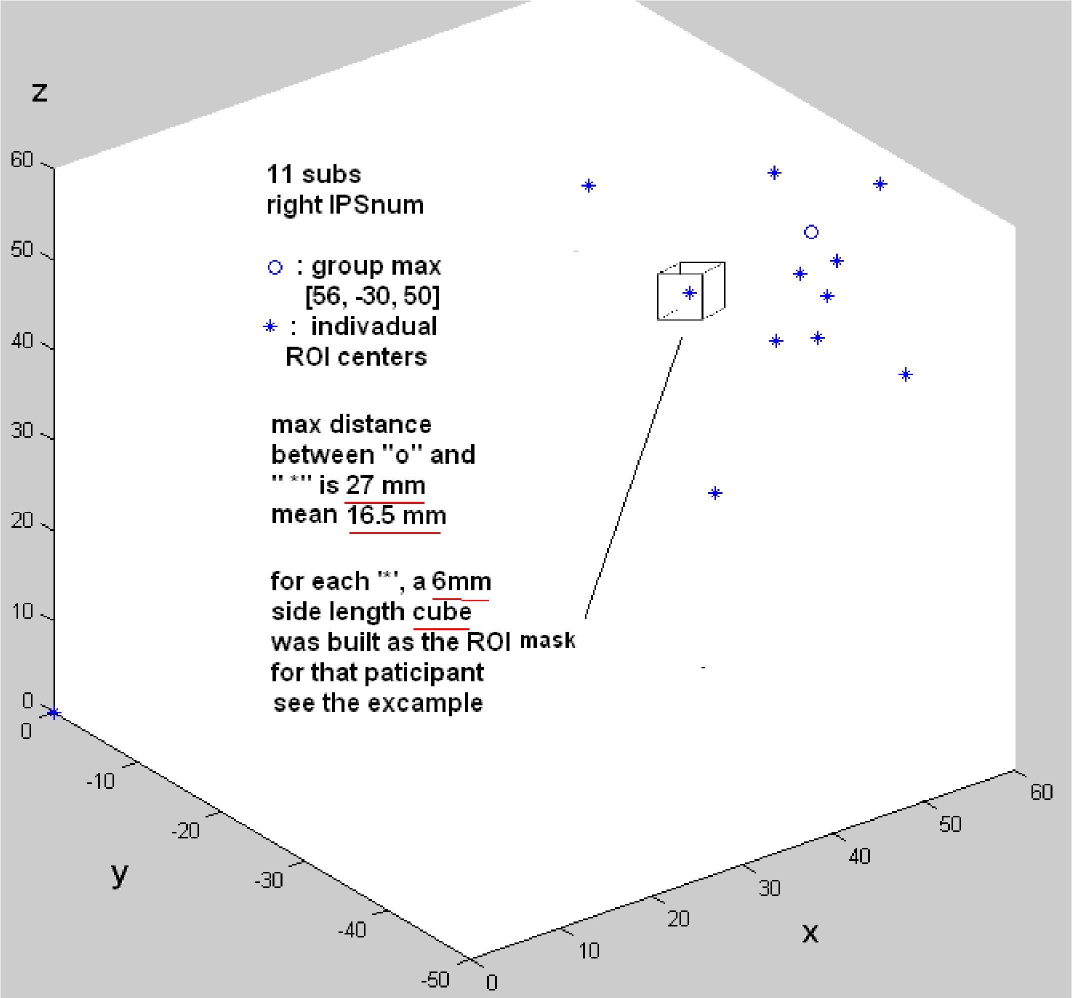


Figure 3.11: The individual number specific ROIs for 10 participants in the right IPSnum

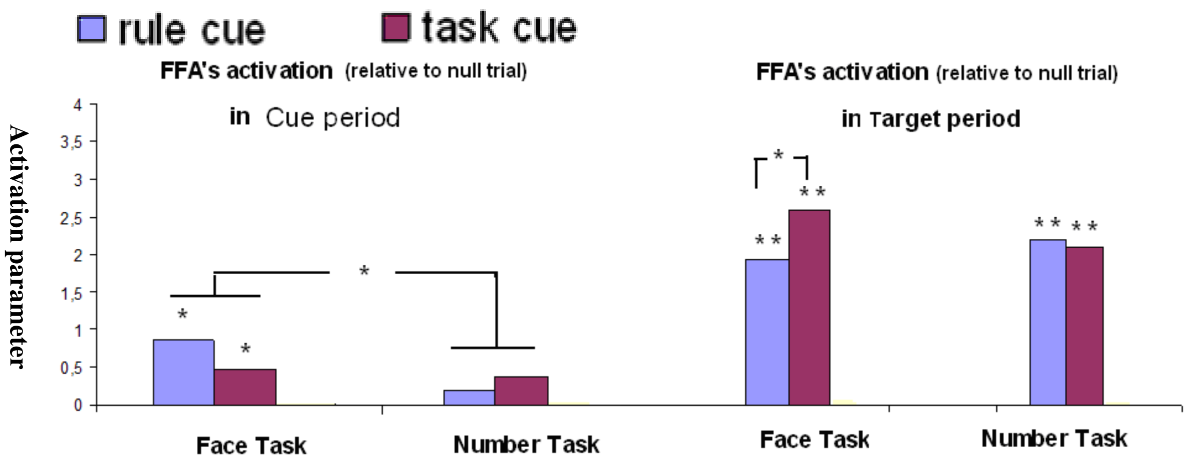
The results of the ROI analysis

As outlined in the Introduction, preparatory attentional modulations were expected to be found in the face and number specific region in face and number task respectively. Then the activation parameters, especially the cue period parameters, of the face specific ROIs (right FFA) and number specific ROIs (right IPSnum) were analyzed.

For the face specific ROIs

Cue period activity:

The activation parameters of cue-only trials were submitted to a 2 x 2 repeated-measures ANOVA with the factors task type (face or number) and cue type (rule-cue or task-cue). Larger activation of the FFA was found for the cue period of the face task compared to the number task (F (1, 11) =6.25, $p<0.05$). Separate T tests showed that both the rule-cue and task-cue elicited significant activity compared to the null trials (t (11) =2.23, $p < 0.05$; t (11) =1.93, $p < 0.05$ (1 tailed; respectively) in the preparation of face task. Whereas no significant activity compared to null trials was found for the preparation of number task in either rule-cue or task-cue condition (both $t < 1.34$, $p > 0.2$). In line with my expectation, these findings indicate preparatory attentional modulation in the face specific regions in both of the two cue conditions.



* p<0.05
** p<0.001

Figure 3.12: Right FFA's activity in cue period and target period

Target period activity

The target period activity in the face specific ROIs was also analyzed. The parameters of target period activation were submitted to a 2 x 2 repeated-measures ANOVA with the factors task type (face or number) and cue type (rule-cue or task-cue). It showed no difference for the activity of FFA between the face and the number task (F (1, 11) = 0.172, p = 0.687). There was no further modulation in the task execution period after the modulation in the preparation period.

The main effect of cue type tended to be significant; in particular, in the target period the activation tended to be larger activation in the task-cue than in rule-cue condition (F (1, 11) = 4.72, p = 0.053).

The interaction of task type and cue type tended to be significant (F (11, 1) = 4.62, p = 0.055); the following separate T tests showed larger activation in the task-cue than in the rule-cue condition of the face task (t (11) = 2.48, p < 0.05), but no difference between these two cue conditions in the number task (t (11) = 0.64, p = 0.53). Finally, significant additional activity was found in the target period in all the task and cue conditions (all ts > 4.5, ps < 0.001).

For the number specific ROIs

As outlined in the method part, the ROIs of number processing were selected from the region of right IPSnum for eleven of the twelve participants. Therefore, the following results are based on the findings of these eleven ROIs in right IPSnum. Important to note that, if including the data of the participant with the left sided ROI into the data set, the results pattern will not change.

Cue period activity:

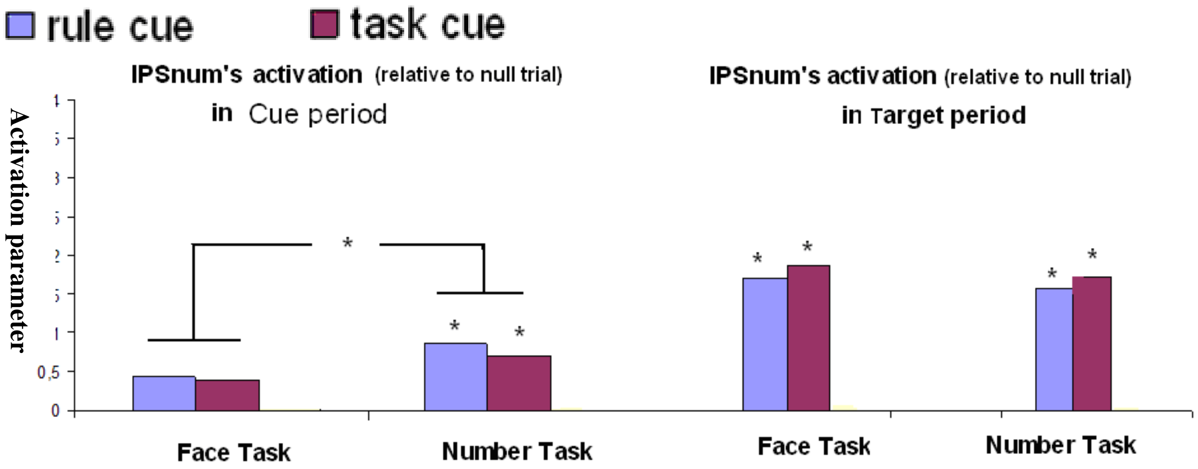
The activation parameters of cue-only trials were submitted to a 2 x 2 repeated-measures ANOVA with the factors task type (face or number) and cue type (rule-cue or task-cue). Larger activation of right IPSnum in the number task than face task in cue period was found ($F(1, 10) = 5.56$, $p < 0.05$). No significant main effect of cue type ($F(1, 10) = 0.08$, $p = 0.78$) was found. Separate t-tests showed that both the rule cue and the task cue tend to elicit additional activity compared to the activity in the null trials ($t(10) = 1.58$, $p = 0.07$; $t(10) = 1.77$, $p = 0.05$ respectively) in the preparation period of the number task. Whereas no additional activity compared to that in null trials was found for the preparation to the face task in either rule-cue or task-cue condition (both $ts < 1.08$, $ps > 0.3$).

Target period activity:

The activation parameters for the target period were submitted to a 2 x 2 repeated-measures ANOVA with the factors task type (face or number) and cue type (rule-cue or task-cue). The main effects of task type and cue type were not significant (both $F<1.5$, both $ps>0.25$): no difference was found for the activity of right IPSnum in face and number task (F

(1, 10) = 1.48, p = 0.25), no difference for the activity in the rule-cue and task-cue condition (F (1, 10) =1.03, p = 0.33) either.

Finally, significant additional activity compared to null trial was found in the target period in all the task and cue conditions (all t > 2.47, p < 0.05).



* p<0.05

Figure 3.13: Right IPSnum's activity in cue period and target period

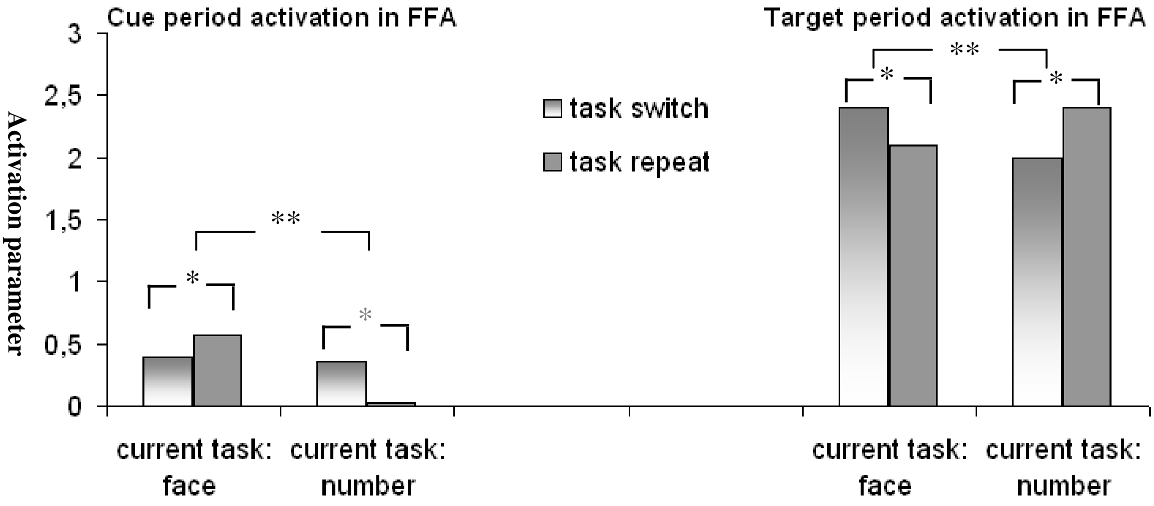
The residual activity in FFA and IPSnum

It has been proposed that subjects have a tendency to perform the same task from one trial to another (Allport et al., 1994). Then on the current trial, there should be residual activity in brain regions selective for the previous task.

Here I describe the findings about a possible influence of the factor task transition on the activation values in the present experiment. FFA's activation parameters, of the cue period and target period respectively, were submitted to a 2 x 2 x 2 repeated-measures ANOVA with the factors of task type (face or number), cue type (rule-cue or task-cue) and task transition (task switch or repetition).

Cue period activity

Significant larger activation was found in the face task than in the number (F (1, 11) = 6.25, p < 0.05). Significant interaction between task type and task transition was found (F (1, 11) = 10.00, p < 0.01). Further T tests indicated that, while participants need to switch from a face task to a number task, larger activity in FFA will emerge as compared to a situation where they repeatedly perform a number task (t (11) = 2.96, p < 0.01); while they repeatedly do a face task, the activity in FFA tends to be larger than when they switch from a number task to face task (t(11) = 1.75, p = 0.054). Probably, these findings indicated that residual activity from the preceding face task still existed in the cue period of current trial, and it thus caused the interaction: when the current task is a face task, larger activation in the repeat than switch condition; when the current task is a number task, larger activation in the switch than repeat condition (Fig. 3.14).



** p<0.01 * p<= 0.05 * p = 0.054

Figure 3.14: Right FFA’s activity in cue period and target period

Target period activity

Significant interaction between task type and task transition was found (F (1, 11) = 11.7, $p < 0.01$). Further T tests indicated that, when the current task is a face task, larger activation was found in the switch than repeat condition (t (11) = 1.76, p = 0.05Whereas when the current task is a number task, larger activation was found in the repeat than switch condition (t (11) = 2.19, $p < 0.05$) (Fig. 3.14). This activity pattern was totally different from the pattern in preparation period which reflected the inertia of preceding trial's activity. So the residual activity didn't persist into the task execution period (and it even seemed to be conquered because the interaction pattern was actually reversed).

Similarly, IPSnum's activation parameters, of the cue period and target period respectively, were submitted to a 2 x 2 x 2 repeated-measures ANOVA with the factors of task type (face or number), cue type (rule-cue or task-cue) and task transition (task switch or repetition).

The only significant effect is the main effect of task type in cue period (F (1, 10) = 5.56, $p < 0.05$). Although there was only a tendency for an interaction of task type and task transition on the activation values (F (1, 10) = 3.28, p = 0.10), the pattern of activation values was the same (see Fig. 3.15) as for the FFA. In particular, in the relevant task, larger activation was found in the task repetition than switch condition (Fig. 3.15, number task part); in the irrelevant task, larger activation was found in the task switch than repetition condition (Fig. 3.15, number task part).

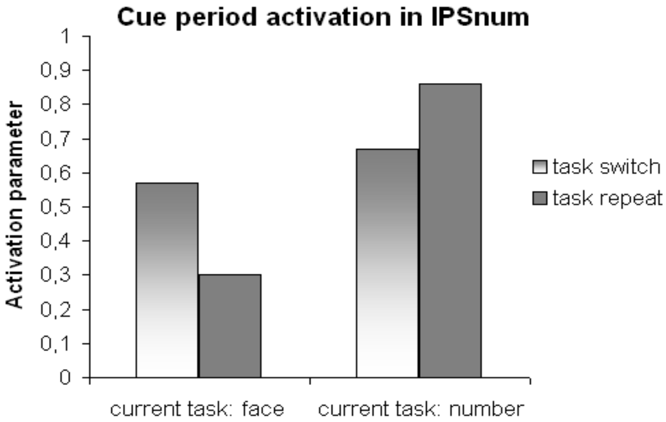


Fig. 3.15

Taking the FFA's and IPSnum's cue period activation together, the results showed that in the current task relevant region, larger activation was found if the current task is the same as the preceding one than different (repetition > switch); whereas in the current task irrelevant region, larger activation was found if the current task is the different from the preceding one than same (switch > repetition). This effect supports that the inertia of the preceding task processing activity could carry over to the current trial. Moreover, note that the same activity pattern didn't appear in the target period, which might indicate the residual activity (or inertia) didn't persist into the task execution.

3.4 Summary of results

In the fMRI Experiment 2, preparatory attentional modulation was found in the face specific and number specific posterior brain regions. In particular, significant additional activity comparing to null trials was found in the preparation period of face task in right FFA; while in the preparation period of number task, significant additional activity comparing to null trials was found in right IPSnum. These findings support the hypothesis that the preparatory attentional control can bias sensory processing via amplifying the activity of the task -relevant stimuls-specificbrain region.

For more details, this amplifying was found both in the rule-cue and task-cue condition, and the amount of activity was not different for the cue types. These results indicate 1) efficient attentional bias occurred in these two cue conditions. As expected, rule-cue and task-cue both supply the information of task type thus can elicit efficient attentional bias. 2) The additional rule information in the display, although it contains the words of the stimuli features (i.e., the drawing of rules for face contains the words of MANN and FRAU; GROSS and KLEIN in the number rule-cue), it failed to elicit additional activity in the relevant specific regions. The participants actually used the whole rule information to activate the task rule, which should be stored in PFC or parietal cortex. Rather than represented single pieces of feature information in the posterior brain regions,

Another interesting finding was: the activity of either FFA or IPSnum in the task execution period was not different for both tasks, which means no attentional modulation in task execution period was found. This finding seems contrary to Serence et al.'s finding (2003). But this finding may suggest that the attentional modulation is not necessarily taking place in the task execution period. For instance, in the present experiment, after the modulation in preparation period, attentional control didn't re-boost in the target period.

Finally, the residual activation from preceding trial still existed in the preparation period of the current trial; such residual activation was found in FFA and IPSnum both. This finding referred to a bottom-up influence in sensory processing. Therefore, in this present experiment, both the attentional modulation (top-down) and the residual activation (bottom-up) could influence the posterior regions' activities.

CHAPTER 4

Experiment 3

4.1 Research aim

This experiment aimed to prove that the learning of task rule from the rule-cue displays only take place when the rules have not yet been obtained well, thus to support the findings of rule implementation in Experiment 1 and 2 were not confounded by some learning processing.

4.2 Method

Subjects

22 right handed healthy students of LMU were recruited. All participants have had normal or corrected-to-normal vision. 11 of them are German (6 male, 21-27 years old), 11 of them are Chinese (5 male, 22-28 years old). They were paid 8 Euros each.

Paradigm and procedure.

The task to be performed by the participants was either gender discrimination (female or male) or number discrimination (bigger or smaller than five, it is called big or small for short).

The task order was unpredictable for the participants. Importantly, the response rules were changing in this experiment (female – left, male – right; small – left, big – right *or* male – left, female - right; big – left, small – right). As shown in Figure 4.1, before each block which contains ten trials, there would be a display to tell the participants the current task rules. The rules could be the same or the reversed comparing to the preceding rules. In this display, the current task rules were plotted, and a central symbol was given to indicate the current rule was kept or changed ("=" for same rule, "X" for changed rule). This display lasted for 5.5 seconds, participants were asked to remember the current task rules and prepare for the following block.

Moreover, each trial in a block was guided by rule-cue or task-cue, thus resulting rule-cue block or task-cue block. Within every block, each trial began with the presentation of a cue (either rule-cue or task-cue) for a fixed duration of 1500 ms. In particular, if the block is a rule-cue block, the rule for current task was given in every cue display, whereas if the block is a task-cue block, no such rule information was given for every trial of this block (see Fig. 4.1). After the presentation of a cue, a target stimulus (face-and-number picture) was displayed for 800 ms, participants were asked to make a response to either the face or number indicated by the cue. Finally, a black screen was displayed for 2700ms after the disappearance of the target.

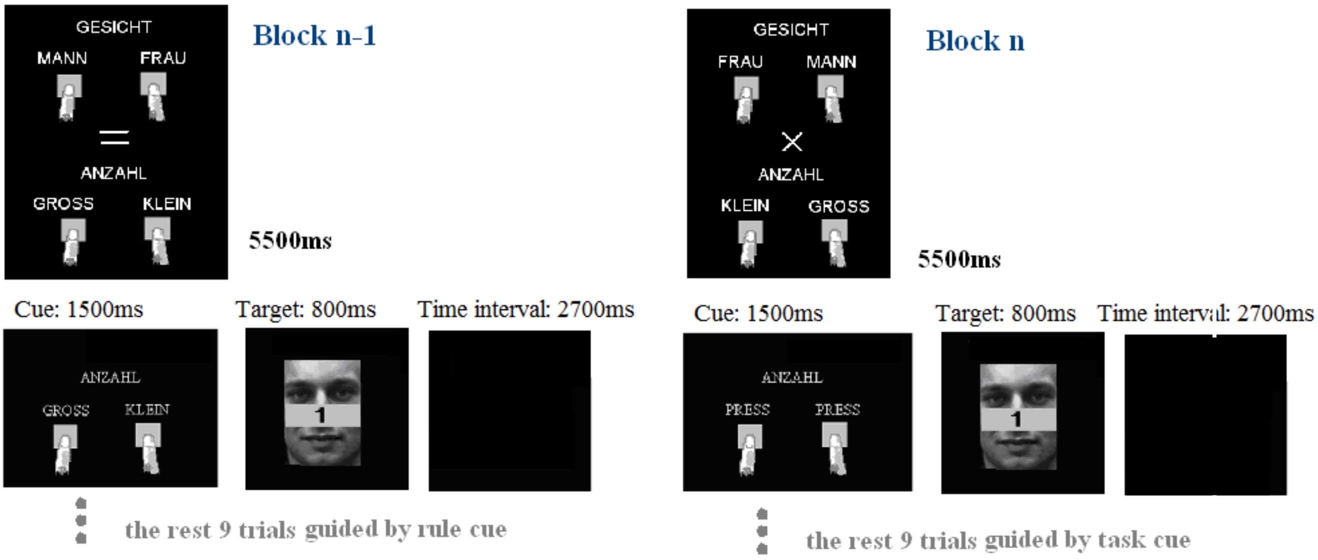


Figure 4.1: Every block started with a display who presents the task rules for the next ten trials. Comparing to the last block's rules, the current task rules could either be the same or reversed. The block could either be a rule cue block (see Block n-1) or a task cue block (see Block n-1). For example, the Block n in this figure is a rule switch_task cue block.

In sum, there were two factors in this experiment. They were rule transition (rule switch or rule repetition) and cue type (rule-cue or task-cue). Totally, 48 blocks were used. Each one of the four conditions: rule switch_rule-cue, rule switch_task-cue, rule repetition_rule-cue, rule repetition_task-cue, had 12 blocks. For instance, the Block n in Figure 4.1 is a rule_switch_task-cue block.

<u>Stimulus and response conditions.</u>

The target stimulus was a face picture with a word of number locating in the region of nose. Two male and two female pictures were used, the number could be "EINS" (one), "ZWEI"(two), "ACHT" (eight) or "NEUN"(nine). As a result 16 face-and-number pictures were used as target stimuli. The same set of target stimuli was used for German and Chinese participants. While the words in the task rule information display and cue display were in German and Chinese, respectively.

All the stimuli, task rule information display before every block, cue stimuli and target stimuli in every trial, were located on a black background in the centre of the screen, and subtended less than 10 degrees, 5 degrees of visual angle respectively.

Participants used their left and right finger for response. They were instructed to respond as fast and as accurately as possible.

4.3. Expectations

For the first few trials of block, a larger rule cue benefit was expected in the rule switch than rule repetition block. Because I expected that the rule cue benefit was contributed by the rule cue facilitation to the processing of rule acquisition and rule implementation both in the rule switch block, whereas it was only produced by the rule cue facilitation to the rule implementation in the rule repetition block However, for the rest trials in a block, even it is a rule switch block, the task rules should been acquired well already. Therefore the rule cue benefit should be produced by rule cue facilitation to rule implementation only no matter the block is a rule repetition or rule switch block. Thus for the rest trials of blocks, identical rule cue benefits were expected for the rule switch and rule repetition block.

4.4 Results

The behavioural data were analyzed with respect to both mean reaction times and error rates. No difference of performance was observed between the German and Chinese participants, thus their date were merged together.

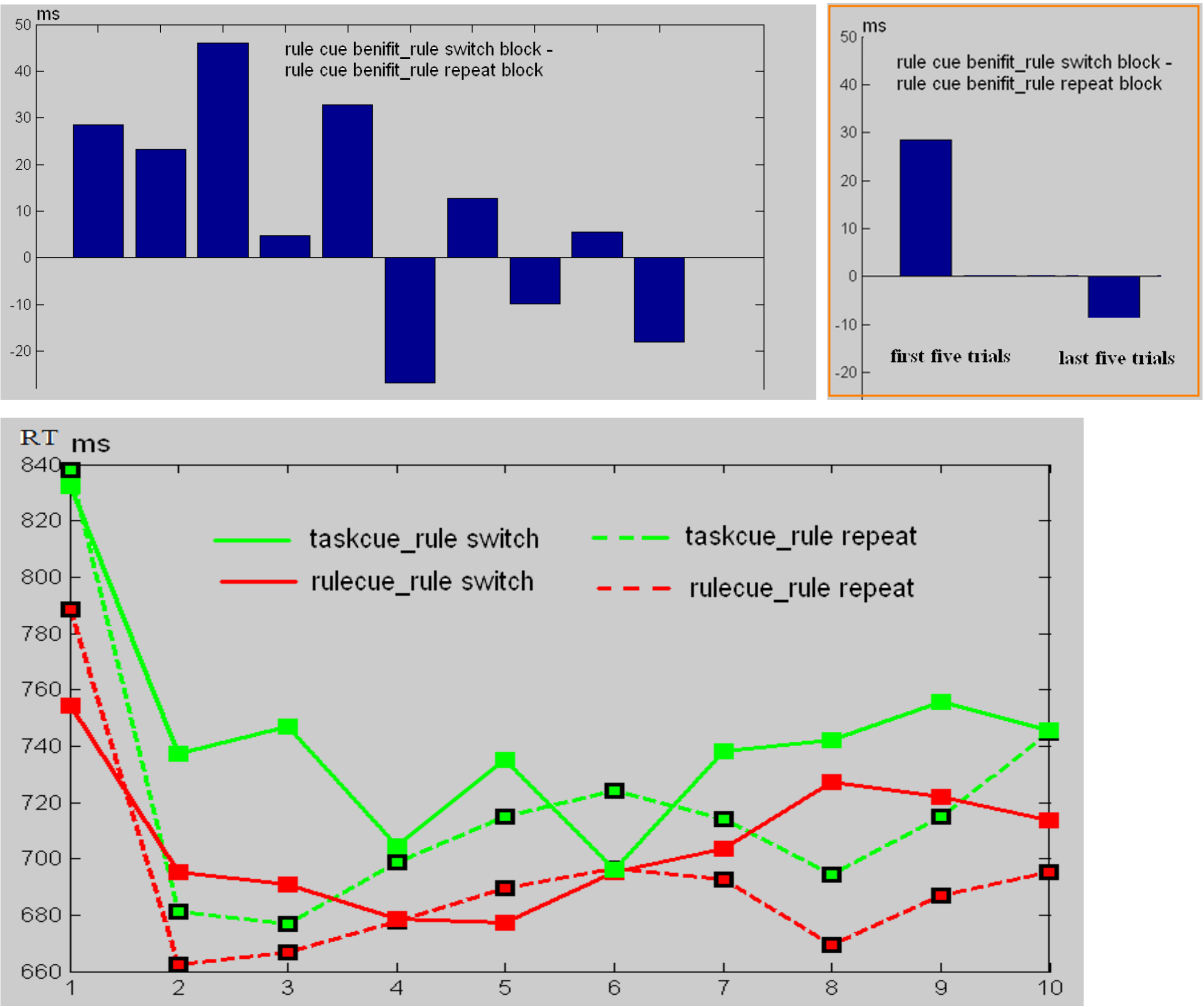


Figure 4.2: The difference between the rule cue benefit in the rule switch and rule repeat block was plotted (Figure 4.2, upper left). As it was expected, more rule cue benefit in the rule switch block than rule repetition block in the first 5 trials, whereas seems identical rule-cue benefit in the last five trials (see Figure 4.2, upper right). For more details, the reaction times of the 10 trials in each condition of block are plotted in the lowest panel. The rule cue benefit was indicated by the difference between red solid and green solid lines for the rule switch block, whereas the rule cue benefit was indicated by the difference between red dotted and green dotted lines for the rule repeat block.

The difference between the rule cue benefit in the rule switch and rule repetition block was plotted (Fig. 4.2, upper left). The results seems fit well with the expectation which assumed more rule cue benefit in the rule switch block than rule repeat block in the first few trials (it turned out to be the first five trials in this study) whereas identical rule-cue benefit in the last few trials (see Figure 4.2, upper right). In order to statistically test the expectations, the data were split into two parts: the first five trials in each block and the last five trials in each block. 2 x 2 repeated-measures ANOVA with rule transition (rule switch vs. rule repetition), and cue type (rule cue vs. task cue) was conducted for the RT and error rate of each part of the data.

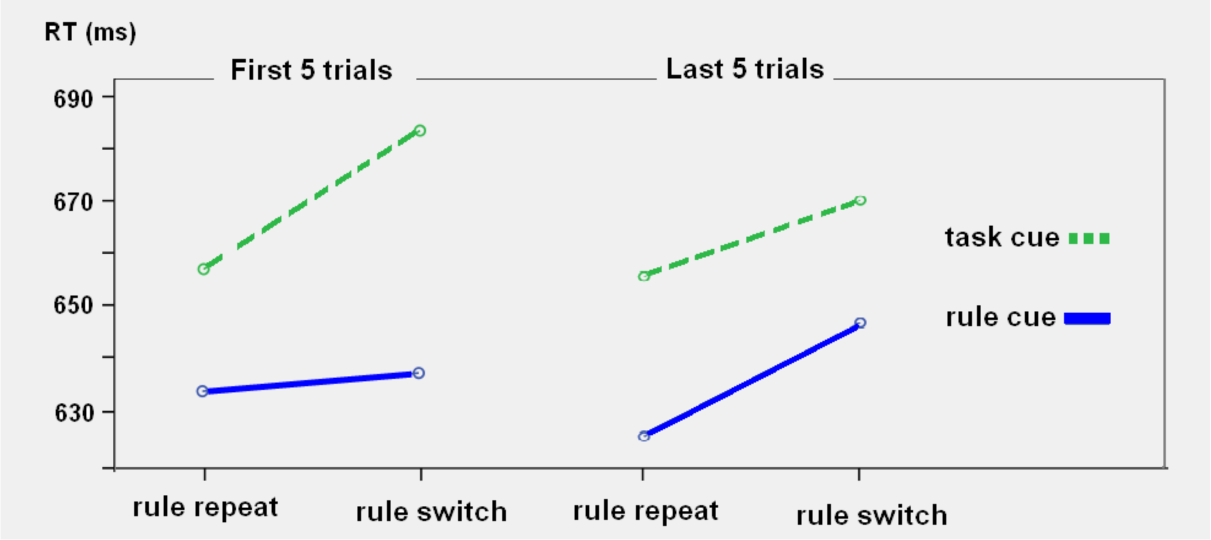


Figure 4.3: Mean RT across conditions for the first and last five trials of blocks

<u>The results of the first five trials in each block</u>

For the RT of correct trials (Fig. 4.3), significant main effect of cue type was found. Subjects are faster when the task is indicated by a rule cue than a task cue (635ms vs. 670ms, F (1, 21) = 14.84, p<0.001). Another, the reaction time in the rule switch condition is slower than in the rule repeat condition (645 vs. 660ms), however this effect failed to be significant (F (1, 21) = 2.66, p=0.118).

In addition and importantly, more rule cue benefit was found in the rule switch than rule repeat condition (23ms vs. 46ms) (figure 12). And corresponding interaction between rule transition and cue type tends to be significant (F (1, 21) = 3.55, p = 0.074). Further t test indicate significant rule cue benefit exist in the rule switch (46ms, t(21) = 3.73, p < 0.001) and in the rule repeat condition (23ms, t(21) = 2.53, p < 0.05). The result indicated that the rule cue benefit was apparently larger in the rule switch blocks than in the rule repeat blocks in the first five trials

For the error rate, the only tend to be significant effect is the main effects of cue type. Less error rate was found when the task is indicated by a rule cue than a task cue (3.8 vs. 5.0%, F (1, 21) = 3.12, p=0.092). Neither the main effect of rule transition (3.2 vs. 4.6%, F (1, 21) = 0.36, p = 0.55) nor the interaction between rule transition and cue type (F (1, 21) = 0.027, p = 0.87) is significant.

The results of the last five trials in each block

For the RT of correct trials (Fig. 4.3), significant main effect of cue type was found. Subjects were faster when the task is indicated by a rule cue than a task cue (636ms vs. 662ms, F (1, 21) = 14.65, p<0.001). In addition, the reaction time in the rule switch condition is significantly slower than in the rule repeat condition (641 vs. 658ms, F (1, 21) = 7.85, p<0.05, =0.011).

As expected, no interaction between rule transition and cue type was found (F (1, 21) = 0.027, p=0.87) (Fig. 4.3), which supported that the rule cue benefit was identical in the rule switch and rule repetition block. Further t tests revealed nearly significant rule cue benefit in the rule switch block (22ms, t(21) = 2.02, p = 0.056) and significant rule cue benefit in rule repetition block (29ms, t(21) = 2.24, p < 0.05).

For the error rate, neither significant main effect nor interaction was found (all Fs < 1.7, all ps > 0.2).

4.4 Summary

As expected, rule cue benefit appeared larger in the rule switch than rule repetition block for the first few trials of blocks. Because the rule cue benefit was contributed by the rule cue facilitation to the processing of rule acquisition and rule implementation both in the rule switch block, whereas it was only produced by the rule cue facilitation to the rule implementation in the rule repetition block.

Moreover, for the rest trials in a block, even it is a rule switch block, the task rules were acquired well already. Therefore the rule cue benefit was produced by the rule cue facilitation to rule implementation only no matter the block was a rule repetition or rule switch block. Correspondingly, for the rest trials of blocks, identical rule cue benefit were found in the rule switch and rule repetition block.

In sum, the findings of this present experiment supported that the learning of task rule from rule-cue displays took place when the task rules have not yet been obtained well (i.e., the first 5 trials in a block with need of task rules re-obtaining).

Note that, the task rules were stable in Experiment 1 and 2, and participants received enough practice before their formal experiment. Therefore, there was no need for the participants to learn the task rule from rule-cue display in the formal experiments, as a result, the learning process had no chance to take place then to confound the findings of rule implementation in Experiment 1 and 2.

CHAPTER 5

General discussion

The present study was interested in two critical components of executive control in the changing task context. In particular, the neural evidence for preparatory attentional bias and the functional neuroanatomy of task rules implementation. To this end, task-cuing paradigm was adopted, in which the changing task context requires general preparation for the upcoming task as well as the flexible activation of the appropriate task rules and attending to appropriate target item.

In order to identify the neural correlates on rule implementation, rule-cue was devised nd applied in the task-cuing paradigm. The rule-cue provides explicit information not only about the type of task to be performed, but also about the specific S-R rule to be applied on the upcoming trial. It was expected to implement the task rule more efficiently than the task-cue who only explicitly supplies task type information in the preparation period. This hypothesis was supported by the behavior rule-cue benefit in the two fMRI experiments and the subtle analysis on the function of rule-cue in Experiment 3. Whereas in the task-cue condition, part of the task rule activation was expected to be postponed into the task execution period and/or more implementation of rule activation was needed. With the comparison between rule-cue and task-cue, the rule-related foci, including the right anterior and middle parts of MFG and SFG, the right IFJ, the pre-SMA, as well as the right SPL and IPL, were isolate from the neural correlates for general task preparation in fMRI Experiment 1. And the region of anterior MFG and SFG, IFJ and pre-SMA again showed to be rule-related in fMRI Experiment 2.

The Experiment 1 of this study was inclined to conclude that the extent to which participants prepare in advance the parameters of a future task depends on the specificity and the amount of information provided prior to task processing. These in turn determines the degree of activation in brain regions associated with task preparation and the following task execution.

In order to find the evidence of attentional preparatory modulation into the stimulus-specific posterior brain regions, the face discrimination and number discrimination tasks were selected the fMRI Experiment 2 because they both have stimulus-specific posterior brain region (i.e. FFA and IPSnum) and they are balanced in task difficulty which encourage participants prepare the two task with similar extent of motivation. And another, both the task relevant and irrelevant feature were presented in the target display in a overlapped rather than spatially separated manner, thus to increase the need of attenional bias in preparation period. As a result, the preparatory modulation was found in the face specific and number specific posterior brain regions. In particular, significant additional activity comparing to null trials was found in the preparation period of face task in right FFA but not in the right IPSnum; while in the preparation period of number task, significant additional activity comparing to null trials was found in right IPSnum but not in the right FA. Further, in the task execution period, no such stimulus-specific modulation was found in either the face or the number task. These findings support the hypothesis that the preparatory attentional control can bias sensory processing via amplifying the activity of the task-relevant stimulus-specific brain region; and suggest that the modulation may not be necessarily needed for task execution if an efficient advanced modulation has been encouraged to take place already.

The Experiment 2 of this study found an attentional modulation of the activities in the posterior stimulus-specific brain regions; meanwhile the activities in these posterior regions were also influenced by the residual activity in the preceding trial. Moreover, the results also suggested that the modulation may not be necessarily needed for task execution if an efficient advanced modulation has been encouraged to take place already.

5.1 Attentional bias, task rule activation and task preparation

The neural correlates

In the present fMRI Experiment 1 and 2, general preparation-related activation is reflected in the activity elicited by cue presentation on cue-only trials, for both the rule-cue and task-cue conditions. The presentation of these cues led to the activation of a large fronto-parietal brain network including the MeFC, the bilateral IFJ, the dorsal and lateral premotor cortices, the medial and lateral parietal lobe, with a relatively smaller magnitude of activation in the bilateral anterior LPFC. This network is largely consistent with that reported in a number of previous studies concerned with the neural correlates of task preparation (Brass & von Cramon 2002, 2004; Gruber et al. 2006; Luks, et al. 2002; MacDonald et al. 2000; Sohn et al. 2000).

According to the preceding image studies, the foci of frontal eye field (FEF) and IPS subtract the preparatory space-based attentional control (e g., Corbetta et al., 2000; Hopfinger et al., 2000; Shulman et al., 1999). And there was some evidence suggested that the object-based preparatory attentional control relys on the same foci also (Shulman et al., 1999; see also Perry & Zeki 2000; Wojciulik & Kanwisher 1999). The large scared lateral frontal and pariatal cortex activated for the general task preparation in exp 1 and 2 involved the FEF and IPS, which should associated with the effort of actively biasing of attention in task preparation. In addition and importantly, in Experiment 1 and 2 of this present study, the rule-related activation foci were a subset of this general task preparation network. In this subset of rule-related regions, the processing of rule (cue) information led to enhanced activation compared to the processing of task (cue) information – as a result of the explicit rule information provided by the rule (but not the task) cues. While rule-cues are as effective as task-cues in activating the general task goal (i.e., the type of task to be performed), they are more powerful in activating the specific task rule. As a result, rule-cues engender superior task preparation compared to task-cues, which is expressed in better performance measures such as response speed and accuracy and in increased neural computations in the related brain regions.

Influential factors for task preparation

There has been a long-standing debate concerning the extent to which participants prepare in advance the (whole) set or only parts of relevant task parameters following cue presentation (Brass & von Cramon 2002; Gruber et al. 2006; Luks, et al. 2002; Ruge et al. 2009; Verbruggen et al., 2007). The present findings suggest that this strongly depends on the amount of explicit task information provided by the cue and the extent of encouraging for advanced task preparation by task setting.

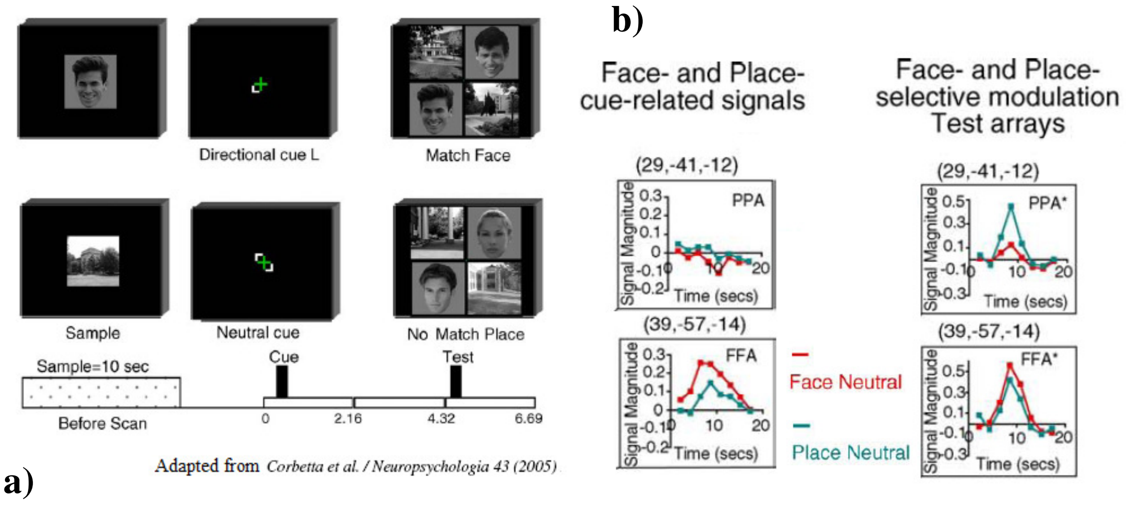
The influence of explicit task information provided by the cue

If the cue contains information about both the type of task and the specific task rules (and if there is sufficient time until the onset of the target), the level of preparedness for the upcoming task will be superior to situations in which the cue does not provide any explicit rule information. Looked at it the other way round, even when the time to prepare would be sufficient as such, participants do not seem to retrieve and/or (sufficiently) pre-activate the (complete) set of task parameters if they are presented with just a task-cue. Rather, a considerable part of the task preparation, in particular, the retrieval and activation of the specific task rule information, appears to be deferred until the presentation of the target.

The experiment setting influence the preparatory modulation in the stimuuls-specific posterior brain regions

In the present fMRI Experiment 2, preparatory modulation has been observed in the face specific and number specific posterior brain regions. However, it is worth to notice that although FEF and IPS were thought to control and modulate the visual sensory processing via amplifies the activity in location-selective and stimulus-specific posterior brain regions. The support of such modulation were not always been found in preceding image studies. In particular, evidence of the space-based preparatory modulation was found in some studies (Kastner et al., 1999; Hopfinger et al., 2000; Ress et al., 2000), but not in some others (Corbetta et al., 2000; 2005). For the object-based preparatory modulation, only partial or weak support for object-based preparatory modulation was found in Wylie et al.'s (2006) and Corbetta et al.' studies (2005). Seeing from the incongruence of findings, one could infer that the occurrence of the attentional modulation may be influenced by several factors. For instance, if the task preparation difficulty is not balanced, then it is hard to find the attentional modulation in the task that is hard to prepare (see Wylie et al., 2006, the motion task, to judge the target bar's speed of rotation is slow or fast, is more difficult than the color discrimination task). As mentioned in the introduction, the task of motion rotation might not easy to imagine then not easy to prepare, and /or the motivation to prepare the hard motion task was not high. Then, it could be suggested that selecting tasks balanced in difficulty may increase the possibility of the occurrence of active preparatory attention modulation.

In spite of the task selection, the particular task setting seems also important for the attentional preparation. For instance, in Corbetta et al.'s 2005 study, participants were asked to do a sample-match task (see Fig. 5.1a). At the beginning of a trial, a sample, either a face or a place, was presented. Later, if the sample was displayed in the test screen, that's a 'match' condition. A cue was given before the test screen to point out one or two positions for the potential target. In this study, the cue period activity of face selective region (FFA) and place selective region (parahippocampal place area, PPA) were analyzed. Only weak stimuli-specific modulation was found in FFA, i.e., larger activation in the preparation for face sample match than place sample match task. And no such modulation was found in PPA. Meanwhile, even no spatially specific pre-activation was found in the retinotopic occipital regions although the cue was spatial.



Adapted from *Corbetta et al. / Neuropsychologia 43 (2005)*

Figure 5.1: a) task setting in Corbetta et al.'s 2005 study

b) FFA and PPA's activation in cue period and target period

These non-robust findings may due to the task setting did not encourage active preparation for either object or space: 1) The face and house pictures are specially dissociated thus not easy to distract each other, which may not hardly encourage the participants bias attention to the target object category. 2) One could infer that the most active preparation participants should include both space-based and object-based attentional control, in particular bias their attention to the one or two position for the potential target (space-based) and to the category of the target (object-based). However it was uncertain that all the participants fully prepared the task in the most active manner. Actually seeing from the results, only weak pre-activation was found in the object-selective visual cortex and no spatially specific pre-activation was found in the retinotopic occipital regions. The only robust pre-activation was found while contrasting the rightward- and leftward-directing cues in a region at the intersection of the IPS and occipital sulcus. Infer from these results, the participants might actively use the directing cue to bias attention to the correct side (left or right), but might not very actively bias their attention to the target object category and the exact location. Because it is easy to find the target in the correct side after the presenting of test display (always one face and one house picture, never need to discriminate two pictures of one category, thus easy to find the target), and after they found the target location, the pictures from the task-irrelevant category could hardly interfere the task (spatially dissociated). Unlike the setting of Cobetta et al.'s study, in the present fMRI Experiment 2, participants only need to do the object-base attentional control, since all the pictures were displayed in a same place (the center of screen), and the task relevant picture was overlapped by the picture of task irrelevant category to increase the interference. These settings could encourage participants biasing their attention to the target category in advance, and correspondingly, preparatory modulations were found in the object-selective posterior brain regions (i.e., FFA and IPSnum).

5.2 Reengagement of executive control involved in preparation period

The rule activation and attentional bias are considered to be critical components of cognitive control in task cuing paradigm. In Experiment 1, the rule related regions activated larger in the rule-cue than task-cue condition, which refer to more sufficient rule activation in the preparation period in the rule-cue condition. In experiment2, preparatory stimulus-specific modulation was found in the face specific and number specific regions, which refer to the efficient preparatory attentional bias. Interestingly, in Experiment 1, the rule implementation regions reengaged more in the task-cue than rule-cue condition, whereas in Experiment 2, no further stimulus-specific modulation was found in the target period, probably because the preparatory modulation was efficient in this study. These findings in Experiment 1 and 2 are in line with some preceding findings: 1) the foci of general anticipatory control (e g., Brass & von Cramon 2002; Gruber et al. 2006) and preparatory attentional control (e g., Corbetta et al. 2000; Shulman et al. 2002b) reengaged in the task execution processing. 2) Similar to the finding of Experiment 2, no attentional modulation was found after efficient preparatory modulation (see Fig 5.1b, FFA’s activity), but if the preparatory attention control failed to biasing the sensory processing in the stimulus-specific region, attentional modulation was found in the target period (see Fig. 5.1b, place specific region PPA’s activity).

All of these finding indicate that the anticipatory cognitive control in the changing task context actually could play role not only when preparing the task but rather whenever it is needed.

5.3 The rule-related regions

LPFC

The present findings indicate that a major region associated with task rule activation is the LPFC. A number of studies that used different paradigms have shown the LPFC to be involved in the maintenance of task-relevant information (e.g., Egner & Hirsch 2005; Kerns et al. 2004; Koechlin et al., 2003; Koechlin & Summerfield 2007; Yeung et al. 2006).

Increased activation in dorsal regions of the LPFC (i.e., DLPFC) related to the maintenance of task rule activation has also been shown for the Stroop paradigm. For example, MacDonald et al. (2000) found neural activity to be increased in the DLPFC when participants were presented with a cue that specified the task coming up next (in the Stroop paradigm). Interestingly, the magnitude of activity increased with the expected difficulty of this task: the DLPFC was more strongly activated when the cue indicated to participants that they would have to process the color of a (color) word, as compared to when it signalled that they would have to process the name of a (color) word. The present findings are in line with these results and they show, additionally, that the degree of activity in DLPFC regions also varies with the amount of specific information provided by the cue about the upcoming task.

An association of rule-relevant processing with regions in the LPFC has been reported in recent fMRI studies by Bunge and colleagues (Bunge et al. 2003; see also Crone et al. 2006a, 2006b). In the Bunge et al. study, participants learned different rules of how to respond to probe stimuli in a separate learning phase prior to the fMRI scanning session. Similar rules (e.g., press left key if two stimuli match each other) were associated with different types of rule-cue (verbal or symbolic cues). In the fMRI scanning session, participants had to activate the acquired rule knowledge upon presentation of the rule-cues and then, after a delay, process two sequentially presented probe stimuli (same, different).

Bunge et al. found ventral regions in the LPFC to be active during the delay after rule-cue presentation, to be sensitive to the difficulty of the rule, and to be insensitive to the type of rule-cue. Because of the insensitivity of these regions to the type of rule-cue, ventral LPFC regions were assumed to be related to abstract rule knowledge; this was in contrast to regions in the DLPFC which proved to be sensitive to the different types of rule-cue and were, therefore, assumed to be related to the specific rule knowledge. These findings are consistent with recent single-cell studies in monkeys in which a similar paradigm was used to assess the representation of rule knowledge in prefrontal regions (Wallis & Miller, 2003; White & Wise, 1999).

While these studies show an involvement of LPFC regions in the retrieval of (abstract and specific) rule knowledge from long-term memory, the present findings show that the degree of rule-related activity may be modulated by the amount of rule information provided by the actual rule-cue. Prior findings were not conclusive about the degree of rule activation in the LPFC because the cues used did not permit distinguishing between general task information and specific rule information (i.e., the different types of information provided by the task and, respectively, rule-cues in the present study).

aPFC

While prior studies of task preparation have mainly reported preparation-related activation in more posterior prefrontal regions, such as near the IFJ and/or the premotor cortex (e.g., Brass & von Cramon 2002, 2004; Gruber et al. 2006), this study found additional preparation-related activation in the right aPFC, and this activation proved to be involved in task rule activation. Findings reported in the literature indicate a critical role of the aPFC for difficult retrieval processes in both episodic-memory (Della-Maggiore et al. 2002; Nyberg et al. 2000; Rajah et al. 1999) and working-memory tasks (Christoff & Gabrieli 2000; Leung et al. 2005; MacLeod et al. 1998; Soto et al. 2007). According to a meta-analysis conducted by MacLeod et al., the right aPFC tends to be activated especially in difficult WM tasks (e.g., when a high, rather than a low number, of items has to be maintained). In particular, the meta-analysis of MacLeod et al. yielded mean activation foci associated with processing in difficult WM tasks which are close (25, 61, 6; Talairach & Tournoux 1988) to the coordinates of the aPFC activation revealed in the present study.

The finding of aPFC activation is also consistent with a study of Stern et al. (2007), who found preparatory activation in the right aPFC in a spatial Stroop task in which the need for rule activation was greater compared to the tasks employed in previous studies (such as those of Brass & von Cramon 2002, 2004; Gruber et al. 2006). In more detail, in Stern et al., participants were presented with a direction-related word (e.g., ‘up’ or ‘down’) on an upper or lower position of the computer screen, and they had to respond to either the direction word or the word location according to a task-cue. Importantly, Stern et al. included only incongruent trials (e.g., respond to the work ‘up’ presented at the lower position), which increased the need for preparatory processes during task-cue processing as compared to studies that intermixed congruent and incongruent conditions. Accordingly, Stern et al. (2007) concluded that the aPFC activation observerd in their study was critical for preparation-related processes in task performance.

Thus, based on these findings, it could be propose that, although the present task was only moderately difficult, the external rule information provided by the rule-cues did enforce the S-R associations to be activated and retrieved from memory to a greater degree than in the task-cue condition. This is the likely explanation for the finding of rule-related activation in the right aPFC in the present paradigm.

IFJ

Activation in posterior regions of the LPFC near the IFJ has been shown to be associated with mechanisms involved in the 'actualization' of the current task representation (e.g., by uploading new task parameters or a new task representation) in situations with changing tasks (Brass & von Cramon, 2004; Derrfuss et al. 2005). The present findings are consistent with this, while additionally showing that the degree to which a new task representation is uploaded in advance depends on the specificity of the information provided by the cue. A larger amount of presented task information permits a more complete uploading of the task parameters required on the upcoming trial, and this is accompanied by an increased amount of neural activity in brain areas near the IFJ.

Rule-related activation outside the lateral prefrontal cortex

Further rule-related activation was found in medial frontal regions and here specifically within the pre-SMA, that is, in regions that are more dorsally located than regions in the anterior cingulate cortex which are associated with mechanisms of conflict detection and/or processing (Carter et al. 2000; Weissman et al.2005). Single-cell and tracer studies suggest that regions of the pre-SMA receive direct input from the LPFC, while the neural regions in the SMA proper are connected to the motor areas (Picard & Strick 2001; Tanji 1994). The specific connections to the LPFC make the pre-SMA most appropriate for the preparation of the specific task rule during sensori-motor performance (Hikosaka et al. 1996). In line with this, several authors have shown the pre-SMA to be involved in the acquisition and control of arbitrary S-R associations in humans (Halsband & Freund 1990; Hikosaka et al. 1996; Gordon et al. 1995; Picard & Strick 1996; Sakai et al. 1998, 1999) and monkeys

(Halsband & Passingham 1985; Halsband et al. 1994). The present study found the pre-SMA to be activated in conditions promoting task rule activation as well as conditions of general task preparation. However, the fact that there was additional activation in the pre-SMA in rule-cue compared to task-cue conditions suggests that providing participants with explicit rule information leads to an enhanced preparation of (specific) S-R associations.

The observation of rule-related activation in the parietal cortex is consistent with the assumption that regions along the intra-parietal sulcus are involved in the activation of motor representations which are spatially mapped to different sensory stimuli (Andersen 1987; Caminiti et al. 1996; Schubert et al. 1998; Stein 1992). A number of neuroimaging studies have revealed parietal activation when participants have to produce motor responses upon the presentation of sensory stimuli in various kinds of behavioral paradigms (Bunge et al. 2002, 2003; Brass et al. 2002, 2004; Zysset et al. 2006; Snyder et al. 1997; Stelzel et al., 2008). The present findings additionally suggest that the parietal involvement is modulated by the amount of prior information provided about the motor response that has to be performed upon stimulus presentation: the more information is provided about the S-R rule, the larger the amount of neural computation in parietal areas involved in processing the required S-R association.

5.4 A higher need of control for the task rule preparation in switch trials

A larger activation was found in exp 1 and 2 during the preparation period (cue-only trials) for task switch compared to task repetition conditions in the medial SFG. This extends findings of other studies, pointing to an association of this region with the switching between tasks (e.g., Dove et al. 2000; Yeung et al. 2006). A related ROI analysis specified that the observed increase of switch-related (compared to repetitions) activation in the medial SFG region was similar in the rule-cue and task-cue conditions. Additionally, the ROI analysis showed that the general amount of activity in switch-related regions was larger with rule-cues than with task-cues. In our view, this latter finding suggests that, given sufficient task rule information, the need to prepare for a task switch evokes efficient processes of reloading the task rule information already during the preparation period of the task processing.

Rule retrieval, or activation of the currently required task set, is presumed to be an important component of task switching (Mayr & Kliegl 2000; Rogers & Monsell 1995, 2003; Rubinstein et al. 2001). In the present study, the task rule information provided by rule-cues may have evoked preparatory processes that included even the rule representation, thus permitting a more complete task set reconfiguration (on switch trials) compared to the presentation of mere task-cues. This would explain why the task switch costs (i.e., error rates) were reduced in the rule-cue relative to the task-cue condition, and why the amount of neural activation was increased in preparation-related regions with rule-cues compared to the task-cues.

Some previous fMRI studies had failed to find any additional region, or even activation, to be involved in preparing for task switches (as compared to repetitions), which was taken to cast doubt on the assumption that switch-specific control processes are operating during the preparation period (Brass & von Cramon 2002, 2004; Gruber et al. 2006; Ruge et al. 2005). I agree that the preparatory processes are comparable in the anticipation of task switches and of repetitions; however, one could suggest that more control is required when preparing for switch trials, and the corresponding additional activation can be found in either the task preparation or the execution period, depending on the type of cue.

A possible reason for the discrepant findings concerning switch-related activations in the preparation period may lie in the different types of cues, or cue information, which were used in studies that failed to and that did find such activations. Studies that failed to find additional switch-related activation (see below) used arbitrary cues (e.g., in Brass et al., 2002, a square or diamond indicating an odd/even and or a number size task), whereas this present study used semantically unequivocal cues to indicate the upcoming task (see also Wylie et al. 2006). It would appear plausible that, if the cue is an arbitrary shape, a considerable amount of time needs to be spent to decode the cue and to represent the general task goal – that is, task rule activation may be delayed and moved to the target period. This might be the reason why studies that used such arbitrary cues failed to find any larger activation in the preparation for task switches compared to repetitions (Brass & von Cramon 2002, 2004; Gruber et al.2006; Ruge et al. 2005). In our study, the word symbol 'gender' indicated the gender task and the symbol 'color' the color task. This use of semantic cues is similar to the conditions in other studies which also reported additional switch-related activity during the preparation period (e.g., Wylie et al. 2006). In the case of semantic cues, the cue specifies the task relatively directly, making it much easier for participants to establish the task representation (Miyake et al. 2004; Wylie et al. 2006) – and permitting them to activate the task rule already within the preparation period. As a consequence, the neural effort associated with the uploading of the task rule information would be increased on task switch compared to repetition trials, and this effort may be strong enough to evoke significant fMRI activation in the comparison of switch versus repetition trials during the task preparation period (Wylie et al. 2006).

5.5 The persistent activity from preceding trials in the posterior brain regions

In the present Experiment 2, residual activation from preceding trial existed in the preparation period in the posterior stimuls-specificbrain regions (i.e., right FFA and right IPSnum). In preview studies for human and monkey, persistent activity was found in PFC, but in the delay period of working memory task (e g., Bunger et al., 2003; Fuster & Alexander 1971; Funahashi et al., 1989, 1990, 1991; Miller et al., 1996). An important difference between the persistent activity in PFC and posterior brain regions is that the former evident an intentional operation for task goal, while the latter is not. Rather the persistent activity could be interference if the current task is not the same as the preceding one. The inertia activity of the preceding trial was claimed to be a important recourse of task switching cost (Allport 1994; Allport & Wylie 1999, 2000), and this opinion was supported by neural evidence from Yeung et al.'s study (2006). In this study, the switch cost was significantly correlated with the amount of activity of the task irrelevant posterior brain regions thus provided a good example on the bottom-up influence for behavior. In the present Experiment 2, preparatory attentional control amplified the activity in the task relevant rather than the irrelevant posterior brain region, meanwhile, the residual activity from preceding task still exist, these two factors together shaped the exact activity pattern in the posterior brain regions. Such findings provided a good example to show the top-down modulation and the bottom-up influence in sensory processing simultaneously.

5.6 Conclusion

This study isolated the neural correlates for task rule implimentation from those related to general task preparation and found an preparatory attentional modulation of the activities in the posterior stimulus-specific brain regions. Moreover, this study was inclined to conclude that the extent to which participants prepare in advance the parameters of a future task in turn determines the degree of activation in brain regions associated with task preparation and the following task execution (i.e. larger activity of rule implementation was found in the task execution period if the rule has not been sufficiently implemented in advance; no attentional modulation of activity in the posterior brain regions was found in the task execution period after a efficient bias of attention in task preparation).

References

Allport DA, Styles EA, Hsieh S (1994) Shifting intentional set: Exploring the dynamic control of tasks. In C. Umilta & M. Moscovitch (Eds.), Attention and Performance XV, pp. 421- 452. Cambridge, MA: MIT Press.

Allport DA, Wylie G (1999) Task-switching: Positive and negative priming of task-set. In G. W. Humphreys, J. Duncan, & A. Treisman (Eds.), Attention, space, and action: Studies in cognitive neuroscience, pp 273-296. Oxford: Oxford University Press.

Allport DA, Wylie G (2000) "Task-switching," stimulus-response bindings, and negative priming. In S. Monsell & J. Driver (Eds.), Control of cognitive processes: Attention and performance XVIII, pp 35-70. Cambridge, MA: MIT Press.

Andersen RA (1987) The role of the inferior parietal lobule in spatial perception and visual-motor integration. In: The handbook of physiology, Sec 1, The nervous system, Vol V, Higher functions of the brain, Ft 2 (Plum F, Mountcastle VB, Geiger SR, eds), pp 483-518. Bethesda, MD: American Physiological Society.

Brass M, von Cramon DY (2002) The role of the frontal cortex in task preparation. Cereb Cortex 12:908-914.

Brass M, von Cramon DY (2004) Decomposing components of task preparation with functional magnetic resonance imaging. J Cogn Neurosci 16:609-620.

Bunge SA, Kahn I, Wallis JD, Miller EK, Wagner AD (2003) Neural circuits subserving the retrieval and maintenance of abstract rules. J Neurophysiol 90:3419-3428.

Bunge SA, Hazeltine E, Scanlon MD, Rosen AC, Gabrieli JD (2002) Dissociable contributions of prefrontal and parietal cortices to response selection. Neuroimage 17:1562-1571.

Bunge SA (2004) How we use rules to select actions: a review of evidence from cognitive neuroscience. Cogn Affect Behav Neurosci 4(4):564-79.

Caminiti R, Ferraina S, Johnson PB (1996) The sources of visual information to the primate frontal lobe: a novel role for the superior parietal lobule. Cereb Cortex 6:319-328.

Carter CS, Macdonald AM, Botvinick M, Ross LL, Stenger VA, Noll D, Cohen JD (2000) Parsing executive processes: strategic vs. evaluative functions of the anterior cingulate cortex. Proc Natl Acad Sci USA 97:1944-1948.

Christoff K, Gabrieli JDE (2000) The frontopolar cortex and human cognition: evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. Psychobiology 28:168-186.

Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman, GL (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nature Neuroscience 3:292-297.

Corbetta M, Kincade JM, Shulman GL (2002) Neural systems for visual orienting and their relationships to spatial working memory. J Cogn Neurosci 14:508–523.

Corbetta M, Tansy AP, Stanley CM, Astafiev SV, Snyder AZ, Shulman GL (2005) A functional MRI study of preparatory signals for spatial location and objects. Neuropsychologia 43:2041-2056.

Crone EA, Donohue SE, Honomichl R, Wendelken C, Bunge SA (2006) Brain regions mediate flexible rule use during development. J Neurosci 26:11239-11247.

Crone EA, Wendelken C, Donohue SE, Bunge SA (2006) Neural evidence for dissociable components of task-switching. Cereb Cortex 16:475-486.

Dehaene S, Piazza M, Pinel P, Cohen L (2003) Three parietal circuits for number processing. Cognitive Neuropsychology 20:487-506.

Della-Maggiore V, Grady CL, McIntosh AR (2002) Dissecting the effect of aging on the neural substrates of memory: deterioration, preservation or functional reorganization? Rev Neurosci 13(2):167-181.

Derrfuss J, Brass M, Neumann J, von Cramon DY (2005) Invovlement of the inferior frontal junction in cognitive control: Meta-analyses of switching and stroop studies. Hum Brain Mapp 25:22-34.

Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. Annu Rev Neurosci 18:193-222.

Dove A, Pollmann S, Schubert T, Wiggins CJ, von Cramon DY (2000) Prefrontal cortex activation in task-switching: an event-related fMRI study. Cogn Brain Res 9:103-109.

Egner T, Hirsch J (2005) Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. Nat Neurosci 8:1784-1790.

Forman S, Cohen J, Fitzgerald M, Eddy W, Mintun M, Noll D (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. Mag Reson Med 33:636-647.

Friston KJ, Holmes AP, Worsley KJ, Poline JP, Frith CD, Frackowiak RSJ (1995) Statistical parametric maps infunctional imaging: a general lineat approach. Hum Brain Mapp 2:189-210.

Funahashi S, Bruce CJ, Goldman-Rakic PS (1989) Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. J Neurophysiol 61:331-349.

Funahashi S, Bruce CJ, Goldman-Rakic PS (1990) Visuospatial coding in primate prefrontal neurons revealed by oculomotor paradigms. J Neurophysiol 63:814-831.

Funahashi S, Bruce CJ, Goldman-Rakic PS (1991) Neuronal activity related to saccadic eye movements in the monkey's dorsolateral prefrontal cortex. J Neurophysiol 65:1464-1483.

Fuster JM, Alexander G (1971) Neuron activity related to short-term memory. Science 173:652-654.

Gollwitzer PM, Sheeran P (2006) Implementation intentions and goal achievement: A metaanalysis of effects and processes. Adv Exp Soc Psych 38:69-119.

Gordon AM, Flament D, Lee JH, Uguibil K, Kim SG, Ebner TJ (1995) Functional MRI of cortical motor areas during sequential typing movements. Abstract 1422. Annual Meeting of the Socirty of Neuroscience. London: MIT Press.

Gruber O, Karch S, Schlueter EK, Falkai P, and Goschke T (2006) Neural mechanisms of advance preparation in task switching. NeuroImage 31:887-895.

Halsband U, Freund HJ (1990) Premotor cortex and conditional motor learning in man. Brain 113:207-222.

Halsband U, Matsuzaka Y, Tanji J (1994) Neuronal activity in the primate supplementary, pre-supplementary and premotor cortex during externally and internally instructed sequential movements. Neurosci Res 20(2):149-155.

Halsband U, Passingham RE (1985) Premotor cortex and the conditions for movement in monkeys (Macaca fascicularis). Behav Brain Res 18(3):269-277.

Hikosaka O, Sakai K, Miyauchi S, Takino R, Sasaki Y, Putz B (1996) Activation of human presupplementary motor area in learning of sequential procedures: A functional MRI study. J Neurophysiol 76:617-621.

Hopfinger JB, Buonocore MH, Mangun GR (2000) The neural mechanisms of top-down attentional control. Nature Neuroscience 3:284–291.

Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302-4311.

Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron 22:751–761.

Kastner S, Ungerleider LG (2000) Mechanisms of visual attention in the human cortex. Annu Rev Neurosci 23:315-341.

Kerns JG, Cohen JD, MacDonald AW III, Cho RY, Stenger VA, Carter CS (2004) Anterior cingulate conflict monitoring and adjustments in control. Science 303:1023-1026.

Koechlin E, Summerfield C (2007) An information theoretical approach to prefrontal executive function. Trends Cogn Sci 11(6):229-235.

Koechlin E, Ody C, Kouneiher F (2003) The architecture of cognitive control in the human prefrontal cortex. Science 302:1181-1185.

Kriegeskorte N, Simmons WK, Bellgowan PS, Baker CI (2009) Circular analysis in systems neuroscience: the dangers of double dipping. Nat Neurosci 12:535-540.

Lavric A, Mizon GA, Monsell S (2008) Neurophysiological signature of effective anticipatory task-set control: a task-switching investigation. Euro J Neurosci 28(5):1016-1029.

Lepsien J, Nobre, AC (2007) Attentional modulation of object representations in working memory. Cerebral Cortex 17(9): 2072-2083.

Leung HC, Gore JC, Goldman-Rakic PS (2005) Differential anterior prefrontal activation during the recognition stage of a spatial working memory task. Cereb Cortex 15(11):1742-1749.

MacDonald AW III, Cohen JD, Stenger VA, Carter CS (2000) Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 288:1835-1838.

MacLeod K, Buckner RL, Miezin FM, Petersen SE, Raichle ME (1998) Right anterior prefrontal cortex activation during semantic monitoring and working memory. Neuroimage 7:41-48.

Mayr U, Kliegl R (2000) Task-set switching and long term memory retrieval. J Exp Psychol Learn Mem Cogn 26:1124-1140.

Meiran N (1996) Reconfiguration of processing mode prior to task performance. J Exp Psychol Learn Mem Cogn 22:1-20.

Meiran N (2000) Modeling cognitive control in task-switching. Psychol Res 63:234-249.

Miller EK and Cohen JD (2001) An integrative theory of prefrontal cortex function. Annu Rev Neurosci 24:167-202.

Miller EK, Erickson CA, Desimone R (1996) Neural mechanisms of visual working memory in prefrontal cortex of the macaque. J Neurosci 16:5154-5167.

Miller RR, Matzel LD (1988) The comparator hypothesis: A response rule for the expression of associations. The psychology of learning and motivation 22:54-60

Miyake A, Emerson MJ, Padilla F, Ahn J (2004) Inner speech as a retrieval aid for task goals: the effects of cue type and articulatory suppression in the random task cuing paradigm. Acta Psychol 115:123-142.

Monsell S (2003) Task switching. Trends Cogn Sci 7:134-140.

Monsell S, Mizon GA (2006) Can the task-cuing paradigm measure an endogenous task-set reconfiguration process? J Exp Psychol Hum Percept Perform 32:493-516.

Nichols T, Brett M, Andersson J, Wager T, Polinee JB (2005) Valid conjunction inference with the minimum statistic. NeuroImage 25:653-660.

Nyberg L, Persson J, Habib R, Tulving E, McIntosh AR, Cabeza R, Houle S (2000) Large scale neurocognitive networks underlying episodic memory. J Cogn Neurosci 12 (1):163-173.

O'Craven KM, Kanwisher N (2000) Mental imagery of faces and places activates corresponding stiimulus- specific brain regions. J. Cogn. Neurosci 12(6): 1013-1023.

Perry RJ, Zeki S (2000) The neurology of saccades and covert shifts in spatial attention: an event-related fMRI study. Brain 123:2273-2288.

Picard N, Strick PL (1996) Motor Areas of the Medial Wall: A review of their location and functional activation. Cereb Cortex 6:342-353.

Picard N, Strick PL (2001) Imaging the premotor areas. Curr Opin Neurobiol 11(6):663-672.

Poline JB, Worsley KJ, Evans AC, Friston KJ (1997) Combining spatial extent and peak intensity to test for activations in functional imaging. Neuroimage 5(2):83-96.

Rajah MN, McIntosh AR, Grady CL (1999) Frontotemporal interactions in face encoding and recognition. Cogn Brain Res 8 (3):259-269.

Ress D, Backus BT, Heeger DJ (2000) Activity in primary visual cortex predicts performance in a visual detection task. Nature Neuroscience 3(9):940–945.

Rogers RD, Monsell S (1995) The cost of a predictable switch between simple cognitive tasks. J Exp Psychol Gen 124:207-231.

Rubinstein JS, Meyer DE, Evans JE (2001) Executive control of cognitive processes in task switching. J Exp Psychol Hum Percept Perform 27:763-797.

Ruge H, Brass M, Koch I, Rubin O, Meiran N, von Cramon DY (2005) Advance preparation and stimulus-induced interference in cued task switching: further insights from BOLD fMRI. Neuropsychologia 43:340-355.

Ruge H, Braver, T, Meiran N (2009) Attention, intention, and strategy in preparatory control. Neuropsychologia 47:1670-1685.

Rushworth MFS, Hadland KA, Paus T, Sipila PK (2002) Role of the human medial frontal cortex in task switching: a combined fMRI and TMS study. J Neurophysiol 87: 2577-2592.

Sakai K, Hikosaka O, Miyauchi S, Sasaki Y, Fujimaki N, Putz B (1999) Presupplementary motor area activation during sequence learning reflects visuo-motor association. J Neurosci 19: RC1(1-6).

Sakai K, Hikosaka O, Miyauchi S, Takino R, Sasaki Y and Pütz B (1998) Transition of brain activation from frontal to parietal areas in visuo-motor sequence learning. J Neurosci 18:1827-1840.

Sakai K, Passingham RE (2003) Prefrontal interactions reflect future task operations. Nat Neurosci 6:75-81.

Sakai K, Passingham RE (2006) Prefrontal set activation predicts rulespecific neural processing during subsequent cognitive performance. J Neurosci 26:1211-1218.

Serences JT, Schwarzbach J, Yantis S (2001) Control mechanisms of object-based visual attention in human cortex. Soc Neurosci Abstr 27:348-349.

Serences JT, Schwarzbach J, Courtney SM, Golay X, Yantis S (2004) Control of object-based attention in human cortex. Cereb Cortex 14:1346-1357.

Serences JT, Yantis S (2007) Spatially selective representation of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. Cereb Cortex 17:284-293.

Schubert T, von Cramon, DY, Niendorf T, Pollmann S, Bublak P (1998) Cortical areas and the control of self-determined finger movements: an fMRI study. NeuroReport 9(14):3171-3176.

Shulman GL, D'Avossa G, Tansy AP, Corbetta M (2002a) Two attentional processes in the parietal lobe. Cerebral Cortex 12(11):1124–1131.

Shulman GL, Ollinger JM, Akbudak E, Conturo TE, Snyder AZ, Petersen SE, Corbetta M (1999) Areas involved in encoding and applying directional expectations to moving objects. J Neurosci 19:9480-9496.

Shulman GL, Tansy AP, Kincade M, Petersen SE, McAvoy MP, Corbetta M (2002b) Reactivation of networks involved in preparatory states. Cerebral Cortex 12(6):590–600.

Snyder LH, Batista AP, Andersen RA (1997) Coding of intention in the posterior parietal cortex. Nature 386:167-170.

Sohn MH, Ursu S, Anderson JR, Stenger VA, Carter CS (2000) The role of prefrontal cortex and posterior parietal cortex in task switching. Proc Natl Acad Sci USA 97:13448-13453.

Soto D, Humphreys GW, Rotshtein P (2007) Dissociating the neural mechanisms of memory-based guidance of visual selection. Proc Natl Acad Sci USA 104(43):17186-17191.

Stein JF (1989) The representation of egocentric space in the posterior parietal cortex. Exp Physiol 74:583-606.

Stelzel C, Kraft A, Brandt SA, Schubert T (2008) Dissociable effects of task order control and task set maintenance during dual-task processing. J Cogn Neurosci 20:613-28.

Stern ER, Wager TD, Egner T, Hirsch J, Mangels JA (2007) Preparatory neural activity predicts performance on a conflict task. Brain Res 11:92-102.

Talairach J, Tournoux P (1988) Co-Planar Stereotaxic Atlas of the Human Brain. Thieme Medical Publishers, Stuttgart-New York.

Tootell RBH, Reppas JB, Dale AM, Look RB, Sereno MI, Brady TJ, Rosen BR (1995) Functional MRI evidence for a visual motion after effect in human cortical area. MT/V5. Nature 375:139-141.

Verbruggen F, Liefooghe B, Vandierendonck A, Demanet J (2007) Short Cue Presentations Encourage Advance Task Preparation: A Recipe to Diminish the Residual Switch Cost. J Exp Psychol Learn Mem Cogn 33:342-356.

Wallis JD, Miller EK (2003) From rule to response: neuronal processes in the premotor and prefrontal cortex. J Neurophysiol 90:1790-1806.

Weissman DH, Gopalakrishnan A, Hazlett CJ, Woldorff MG (2005) Dorsal anterior cingulate cortex resolves conflict from distracting stimuli by boosting attention toward relevant events. Cereb Cortex 15:229-237.

Wendelken C, Bunge SA, Carter CS (2008) Maintaining structured information: an investigation into functions of parietal and lateral prefrontal cortices. Neuropsychologia 46(2):665-78.

White IM, Wise SP (1999) Rule-dependent neuronal activity in the prefrontal cortex. Exp Brain Res 126(3):315-335.

Wojciulik E, Kanwisher N (1999) The generality of parietal involvement in visual attention. Neuron 23:747-764 (1999).

Wylie GR, Javitt DC, Foxe JJ (2006) Jumping the gun: is effective preparation contingent upon anticipatory activation in task-relevant neural circuitry? Cereb Cortex 16:394-404.

Yeung N, Nystrom LE, Aronson JA, Cohen JD (2006) Between-task competition and cognitive control in task switching. J Neurosci 26(5):1429-1438.

Zeki S, Watson JD, Lueck CJ, Friston KJ, Kennard C, Frackowiak RS (1991): A direct demonstration of functional specialization in human visual cortex. J Neurosci 11:641–649.

Zysset S, Wendt CS, Volz KG, Neumann J, Huber O, von Cramon DY (2006) The neural implementation of multi-attribute decision making: a parametric fMRI study with human subjects. Neuroimage 31:1380-1388.

German summary

Deutsche Zusammenfassung

Die vorliegende Arbeit behandelt zwei bedeutende Bestandteile der exekutiven Kontrolle, nämlich die funktionelle Neuroanatomie bei der Aktivierung von Aufgaberegeln und die vorbereitende Verschiebung der Aufmerksamkeit, im Kontext von wechselnden Aufgaben. Dabei wurde das task-cuing Paradigma angewandt, bei dem wechselnde Aufgaben eine flexible Verschiebung der Aufmerksamkeit auf ein geeignetes Ziel sowie eine Aktivierung der geeigneten Aufgabenregeln erfordert.

Um die funktionelle Neuroanatomie der Aktivierung von Aufgaberegeln zu finden, wurde das fMRI Experiment 1 durchgeführt, wobei die Experimentalbedingung „rule-cue“ zum Modulieren des Grades der Aktivierung von Aufgaberegeln gewählt wurde.

Während bei bisherigen Studien die Anwendung einer „task-cue“-Bedingung nur Informationen über den Typ der zu erfüllenden Aufgabe bot, liefert die Anwendung der „rule-cue“-Bedingung darüber hinaus auch Informationen über die spezifische Stimulus-Respone-Regel, die auf die folgende Aufgabe anzuwenden ist.

Bei Anwendung der „rule-cue“-Bedingung wurde eine bessere Aktivierung der Aufgabenregeln in der Vorbereitungsperiode erwartet. Hingegen wurde bei Anwendung der „task-cue“-Bedingung erwartet, dass ein Teil der Aktivierung der Aufgabenregeln in die Phase der Aufgabeausführung, nämlich nach der Präsentation des Zielobjektes, verschoben werden könnte. Das Experiment konnte tatsächlich zeigen, dass die Reaktionszeiten der Versuchspersonen bei Verwendung der „rule-cue“ kürzer und die Fehlerquote auch niedriger waren als bei der „task-cue“.

Im fMRI Experiment 1 zeigten sich während der Vorbereitungsphase höhere Aktivierungen in der „rule-cue“-Bedingung als in der „task-cue“-Bedingung im vorderen und mittleren Teil des rechten mittleren frontalen Gyrus (MFG) und des superioren frontalen Gyrus (SFG), im rechten inferioren frontalen Knotenpunkt (IFJ), im präsupplementären motorischen Areal (pre-SMA) sowie im rechten superioren parietalen Lobus (SPL) und im inferioren parietalen Lobus (IPL).
Zudem ließ sich in der Phase der Aufgabenausführung, d.h. während der Präsentation des Zielobjekts, in diesen Regionen eine höhere Aktivierung in der „task-cue“-Bedingung als in der „rule-cue“-Bedingung beobachten. Zusammenfassend ließen sich im fMRI Experiment 1 neuronale Korrelate der Aktivierung von Aufgaberegeln finden und es ließ sich zeigen, dass diese Korrelate eine Teilmenge des Gehirnnetzwerks für die allgemeine Vorbereitung auf Aufgaben sind.

Im fMRI Experiment 2 ließ sich die vorbereitende Verschiebung der Aufmerksamkeit in posterioren Gehirnregionen finden, die auf die Verarbeitung von Gesichtern bzw. von Zahlen spezialisiert sind. Insbesondere zeigte sich in der Vorbereitungsphase einer Gesichter-Aufgabe im rechten FFA eine signifikante zusätzliche Aktivierung im Vergleich zu Null-Trials. Bei einer Zahlen-Aufgabe hingegen zeigte sich im rechten IPSnum eine signifikante zusätzliche Aktivierung im Vergleich zu Null-Trials. Diese Ergebnisse stützen die Hypothese, dass die vorbereitende Kontrolle der Aufmerksamkeit die sensorische Verarbeitung beeinflussen kann, indem sie die Aktivität der für die spezifischen Stimuli der Aufgabe relevanten Gehirnregionen verstärkt.

Diese Verstärkung wurde sowohl unter der „rule cue“- als auch unter der „task cue“-Bedingung gefunden und der Grad der Aktivierung variierte nicht bei den beiden

Bedingungen. Die Ergebnisse verdeutlichen, 1) dass eine effiziente Verschiebung der Aufmerksamkeit bei beiden „cue“-Typen geschieht. Wie erwartet, liefern sowohl die „rule cue“-Bedingung als auch die „task cue“-Bedingung Informationen über den Typ der Aufgabe und ermöglichen damit die effiziente Modulation der Aufmerksamkeit. 2) Die zusätzlichen Informationen über die Aufgabenregeln unter der „rule-cue“-Bedingung konnte keine zusätzliche Aktivierung in den relevanten spezifischen Regionen auslösen, obwohl sie die relevanten Stimuli-Besonderheiten verbalisierte (d.h. die „rule-cue“ der Gesichter-Aufgabe enthielt die Worte MANN und FRAU, die „rule-cue“ der Zahlenaufgabe enthielt die Worte GROß und KLEIN). Die Versuchspersonen wenden die gesamte Information über die Regeln an, welche im PFC oder im parietalen Kortex gespeichert sein sollte, um die Aufgabenregel zu aktivieren und nicht einzelne Bruchstücke der Information auf dem Display.

Eine weitere interessante Beobachtung war: es wurde während der Phase der Aufgabenausführung weder im FFA, noch im IPSnum eine Verschiebung der Aufmerksamkeit gefunden, d.h. die Aktivierung des FFA in der Phase der Aufgabenausführung war identisch mit jener in der Gesichter- und der Zahlen-Aufgabe. Dies könnte bedeuten, dass die Kontrolle der Aufmerksamkeit nach einer effizienten vorbereitenden Aufmerksamkeitsmodulation nicht noch einmal verstärkt wird in der Phase der Ausführung.

Zusätzlich zu der Verschiebung der Aufmerksamkeit beeinflusste die verbleibende Aktivierung vom vorangegangenen Trial die Aktivierung der posterioren Gehirnregionen (d.h. die Aktivierung des FFA während der „cue“-Phase war höher, wenn die vorangegangene Aufgabe eine Gesichter-Aufgabe war, als wenn sie eine Zahlen-Aufgabe war). Dieses Experiment stellt ein gutes Beispiel dar, um die top-down-Modulation der

Aufmerksamkeit und den bottom-up-Einfluss der sensorischen Verarbeitung gleichzeitig zu demonstrieren.

Das dritte Experiment sollte die Funktion der „rule-cue“ zeigen und die Ergebnisse zur Regelaktivierung, die in Experiment 1 und 2 gefunden worden waren, stützen. Es ließ sich zeigen, dass die „rule-cue“ Bedingung sowohl den Erwerb als auch die Anwendung einer Regel erleichtern kann, jedoch ist nur die Erleichterung der Anwendung längerfristig. Insbesondere kann die explizite Information über die Regel, bevor die Regeln gut verinnerlicht sind, die Versuchspersonen direkt und zum richtigen Zeitpunkt an die Regel erinnern und ihnen das Merken der Regel erleichtern. Jedoch wird die explizite Information über die Regel nach ein paar Trials überflüssig, weil die Aufgabenregeln schnell und gut gemerkt werden können. Auf der anderen Seite könnte die „rule-cue“-Bedingung die Anwendung der Regel erleichtern, unabhängig davon, ob die Regel bereits erworben wurde. Im Hinblick auf die Langfristigkeit dieser beiden Vorteile, kann man von einer kurzfristigen Erleichterung des Regelerwerbs und von einer längerfristigen Erleichterung der Regelanwendung ausgehen. Die Vorteile der „rule-cue“-Bedingung in den fMRI Experimenten 1 und 2 spiegelten hauptsächlich die Erleichterung der Regelanwendung durch die „rule-cue“ wieder.

Acknowledgments

This dissertation was written at the Ludwig-Maximilians University in Munich. During the course of my dissertation, I am a student supported by the CSC-LMU project which is cooperation between China Scholarship Council and Ludwig-Maximilians University.

I am grateful for all the support and help I have received whilst researching and writing up this dissertation. Thanks especially go to Prof. Torsten Schubert, who supported and supervised me every step of the way. I also want to express my special gratitude to Prof. Hermann J. Müller for his support and encourage. Thanks Prof. Dr. Susanne Weber for attending my defence as a committee member and asking questions associated to business education. In addition, thank to Prof. Xiaolin Zhou, Chen Qi and Hou Ran for their help on the conducting, designing and data analyzing of Experiment 1. Thanks also address to Ute Coates and Thomas Meindl for help in the data collecting of Experiment 2; to Ding Yong and Angelika Reich for their help on the German summary; to Sun Luning for help in Experiment 3's running; to Zhou Zhiliang for support in the final stage of the thesis writing.

Last but not least, I would like to thank my parents Shi Wanqing and Chen Yingke for their endless support during the past years.

Shi Yiquan

Munich, December 2009

Curiculum Vitae

Personal Information

Name: Yiquan Shi
Place of birth: Hu Nan, China
Gender: Female
Date of birth: 31/05/1981
Tel: (+49) 89 2180 5159
Fax: (+49) 89 2180 5211
Email: ssyyqq.s@gmail.com
Address: Room 2105, Leopoldstr. 13, 80802 München

Education

2006/09 – 2009/12	**Doctoral student** in Department of Psychology, Ludwig Maximilians University, Munich. Supervised by Prof. Dr. Torsten Schubert and Prof. Dr. Herman Müller, funded by the Chinese Scholarship Council, Ludwig-Maximilians-Universität (**LMU**) Munich – China Scholarship Council (**CSC**) Program
2006/06	**Master degree** in Basic Psychology, Peking University, Beijing
2003/09-2006/06	Study of cognitive psychology at Peking University. Supervised by Prof. Dr. Xiaolin Zhou
2003/06	**Bachelor degree** in information and computing science, Central South University, Changsha
1999/09-2003/06	Study of information and computing science at Central South University

Supplemental material

The preliminary behavioral experiment for Experiment 2

The experiment procedure was the same as the procedure of fMRI Experiment 2.

Seventeen right-handed, healthy students of University participated in the study. They were paid 6 Euros for their service.

Results

Mean RTs were submitted to a 2 x 2 x 2 repeated-measures ANOVA with the factors task type, cue type and task transition. No significant effect was found for the main effect of task type (772 vs. 755ms, F (1, 16) = 1.36, p =0.26). RTs were significantly faster in the rule-cue than in the task-cue condition (main effect of cue type, F (1, 16) = 11.61, p < 0.005), which indicates that participants effectively utilized the rule-cue information during the preparation period following cue presentation. The RT advantage for rule-cue compared to the task-cue presentation (i.e., the 'behavioral rule-cue effect') was 16 ms. In addition, RTs were significantly slower for task switch than for task repetition trials (main effect of task transition, F (1, 16) = 24.79, p < 0.0001, 32ms switch cost). No significant interaction was found.

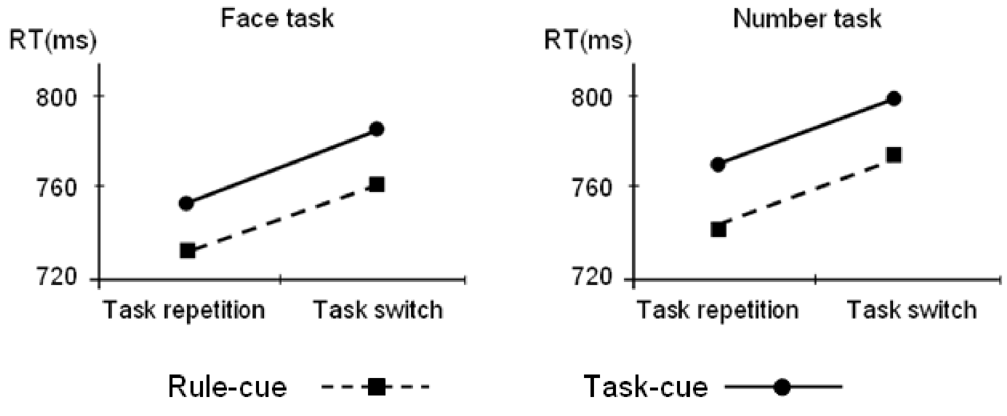


Fig 1. RTs as function of task transition and cue type in face and number task

Mean error rates were submitted to a 2 x 2 x 2 repeated-measures ANOVA with the factors task type, cue type and task transition. No significant effect was found for the main effect of task type (F (1, 16) = 1.586, p =0.23). Error rates were not differed by task type (4.7% vs. 6.0%, F (1, 16) = 1.59, p = 0.23). Error rates were lower in the rule-cue than in the task-cue condition (4.7% vs. 6%, main effect of cue type tends to be significant, F (1, 16) = 3.70, p = 0.072. In addition, error rates were significantly higher for task switch than for task repetition trials (6.2% vs. 4.5%, main effect of task transition, F (1, 16) = 18.57, p < 0.001). No significant interaction was found.

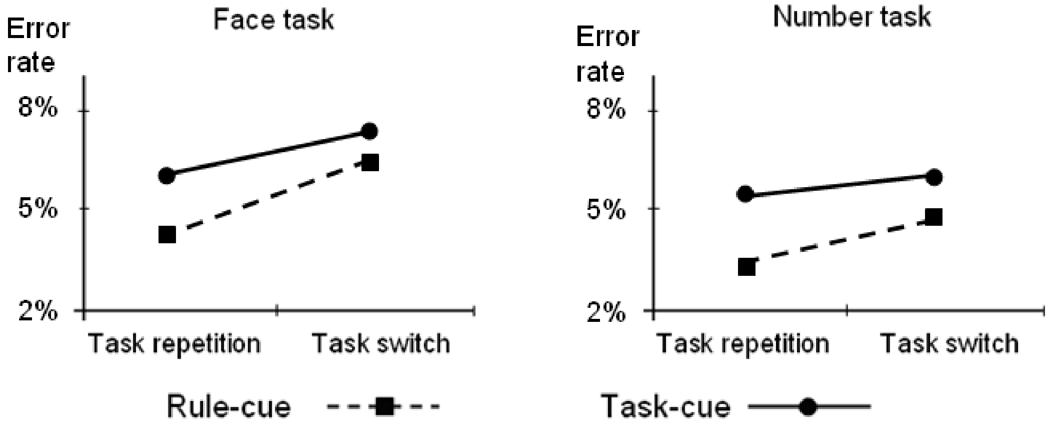


Fig 2. Error rates as function of task transition and cue type in face and number task

In sum, the behavioral performances (RT and error rates) were identical in gender discrimination and number discrimination tasks. Therefore the task difficulties are balanced in these two tasks.