BRAIN RESEARCH 1374 (2011) 90–99

available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research Report

Two successive neurocognitive processes captured by near-infrared spectroscopy: Prefrontal activation during a computerized plus-shaped maze task

Hiromtisu Miyata[a,b,*], *Shigeru Watanabe*[b], *Yasuyo Minagawa-Kawai*[c]

[a]*Japan Society for the Promotion of Science, Tokyo, Japan*
[b]*Department of Psychology, Keio University, Tokyo, Japan*
[c]*Graduate School of Human Relations, Keio University, Tokyo, Japan*

ARTICLE INFO

Article history:
Accepted 11 December 2010
Available online 21 December 2010

Keywords:
Planning
Maze
Touch-sensitive screen
Inhibition
Prefrontal cortex
Near-infrared spectroscopy

ABSTRACT

The present study using near-infrared spectroscopy (NIRS) examined prefrontal activation associated with maze-solving performance in adult humans. The participants were required to solve a plus-shaped maze, comparable to the one used for pigeons and human children to behaviorally assess planning processes, by moving a target square to a goal square presented on a touch-sensitive screen. The participants made incorrect responses toward a previous goal immediately after the goal jumped to the end of another arm, in parallel with but less frequently than previous participants, with shorter reaction times than when they correctly adjusted their responses. In these incorrect trials, relatively larger hemodynamic changes having two peaks were observed, especially in channels near the right inferior frontal cortex (IFC), suggesting use of additional cognitive resources for adjustment of responses after making errors. In addition to showing human adults' better behavioral inhibition than previous participants, the present NIRS data suggest a difference in prefrontal activation patterns according to whether inhibition of the forward plan was working well or not. The results also testify to the effective NIRS recording, while the participants were moving a computer-generated stimulus by actually making finger touches to the monitor.

1. Introduction

Planning, the internal processes of formulating an organized method about one's future behavior, is important for both humans and non-human animals because it seems to underlie many daily activities. Studies of human patients with decreased prefrontal cortex function have shown that performance on planning tasks like the Tower of London task are impaired especially when the task complexity is increased, suggesting involvement of prefrontal cortex in human planning (e.g., Shallice, 1982; Dagher et al., 1999; Veale et al., 1996; Pantelis et al., 1997). A number of more recent neuroimaging studies have also addressed the neural correlates of human planning in virtual situations and suggested that the prefrontal cortex, as well as other brain regions such as the premotor, cingulate, and insular cortices and striatum, may play a central role in

* *Corresponding author*. Department of Psychology, Keio University, 2-15-45 Mita, Minato-ku, Tokyo 108-8345, Japan. Fax: +81 3 5427 1578.
E-mail address: miyatahiromitsu@gmail.com (H. Miyata).

0006-8993/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2010.12.047

cognitive planning in humans (Owen, 1997; Robbins, 1998). As a neuronal network model by Dehaene and Changeux (1997) suggested, different subprocesses or neural circuits may contribute to different levels of planning. This seems to support the view that regional activation patterns could differ according to different planning levels (e.g., Baker et al., 1996; Dagher et al., 1999; van den Heuvel et al., 2003), although evidence from these preceding studies to date is not consistent.

Although planning was believed to be unique to humans till recent years (Tulving, 1983; Suddendorf and Corballis, 1997), recent behavioral and neurophysiological studies suggest that not only humans but also a number of non-human primates (e.g., Biro and Matsuzawa, 1999; Iversen and Matsuzawa, 2003; Kawai and Matsuzawa, 2000; Fragaszy et al., 2003; Mulcahy and Call, 2006; Mushiake et al., 2006; Shima et al., 2007) and birds (e.g., Emery and Clayton, 2001; Raby et al., 2007; Correia et al., 2007; Miyata et al., 2011) may possess planning abilities at a certain level. In this frontier, Miyata et al. (2006) explored planning abilities in pigeons (*Columba livia*) behaviorally by training them to navigate a red square (the target) to a blue square (the goal) by pecking, before exposing them to a variety of detour tasks. Next, Miyata and Fujita (2008), using a plus-shaped maze and variations thereof, found that pigeons planned future behavior both while solving the maze and before starting to solve the maze, in a test in which the target jumped to another corner either during task solution or immediately after the preview phase (see also Miyata and Fujita, 2010). We also modified these maze tasks to test 3- to 4-year-old children, which yielded data in parallel with those obtained from pigeons (Miyata et al., 2009). These data suggested that a number of avian species may possess basic planning capacity, which may be shared across taxa.

In the present study, we examined prefrontal activation associated with different levels of planning in adult humans. We used a plus-shaped maze task presented on a touch screen previously used to test human children and pigeons. Virtual spatial navigation or maze tasks have been extensively employed in human imaging studies using positron emission tomography (PET) (e.g., Ghatan et al., 1995) and functional magnetic resonance imaging (fMRI) (e.g., Antonova et al., 2009; Folley et al., 2010; Iaria et al., 2009; Moffat et al., 2006) to examine patterns of brain activation associated with visuo-spatial skill, ability to obey rules, and route planning. We used near-infrared spectroscopy (NIRS), a non-invasive neuroimaging technique, to measure hemodynamic responses in the cerebral cortex (Maki et al., 1995; Minagawa-Kawai et al., 2009). Using NIRS allows examination of brain activity in a more natural situation in which daily cognitive activities are implemented and does not require immobilization like PET and fMRI. In addition, evidence from neuronal imaging in human adults would provide valuable data prior to investigating patterns of activation associated with planning in both non-human species and human children in comparable settings.

The aim of the present NIRS study was to evaluate prefrontal activation associated with planning using a computerized plus-shaped maze task. As in previous studies with pigeons (Miyata and Fujita, 2008) and children (Miyata et al., 2009), we introduced a condition in which the goal suddenly jumped to the end of one of the other arms while the participants were solving the maze. We hypothesized three levels of planning in this situation: (1) no planning, (2) planning without adjustment to change, and (3) planning with adjustment to change. When the participants do not plan future behavior (1), though this case may not be plausible in human adults, change of the goal locations would not affect their performance. When subjects plan future behavior but have difficulty adjusting their behavior after the goal-change (2), they would move the target in the direction of the previous goal at the center of the maze. In this case, latency of response immediately after the goal-change should be no different from or shorter than that in the control condition. Finally, when subjects plan future behavior and flexibly adjust their behavior as well (3), they would take correct routes as in (1), but with longer response times than in the control condition. We expected to find differences in cortical activation patterns associated with these different levels of planning.

2. Results

2.1. *Behavioral results*

Analysis was done for the 36 test trials, in the same ways as described by Miyata and Fujita (2008) and Miyata et al. (2009). Fig. 2A shows the proportions of the next movement directions of the target when it was at the center of the maze. Proportions of correct responses were significantly lower in the goal-change than in the same-goal condition (Wilcoxon signed-rank test; $Z\,[N=20]=-3.830$; $p=.000$). All the errors in the goal-change trials were toward the previous goal locations. Three participants made no change-correct responses and one made no change-error responses. Thus, the participants frequently moved the target toward the previous goal location after the goal jumped to another corner in the goal-change condition, which resulted in poorer performance at the center point in the goal-change than in the same-goal condition.

Fig. 2B shows response time (latency of response) when the target was at the center of the maze, that is, latency between the moment when the target stopped at the center of the maze after the previous movement and the moment when the touch to the guide dot was made for the next movement. Movements toward "other directions" (three trials in the same-goal condition) were excluded from analysis. The remaining trials were divided into three response types: for the same-goal condition, response time for correct movements was considered (i.e., same-correct), while for the goal-change condition trials were divided based on whether they were incorrect movements toward the previous goal location (i.e., change-error) or correct movements toward the goal after the change of location (i.e., change-correct). A one-way repeated-measures ANOVA revealed a significant effect of response type ($F\,[2, 30]=34.009$, $p=.000$). Multiple comparison tests with Bonferroni correction revealed significant differences between same-correct and change-error ($p=.000$), between same-correct and change-correct ($p=.004$) and between change-error and change-correct ($p=.000$). These data show that, in the change-error trials, response time was shorter than that in the same-correct trials, while in the change-correct trials, response time was relatively longer.

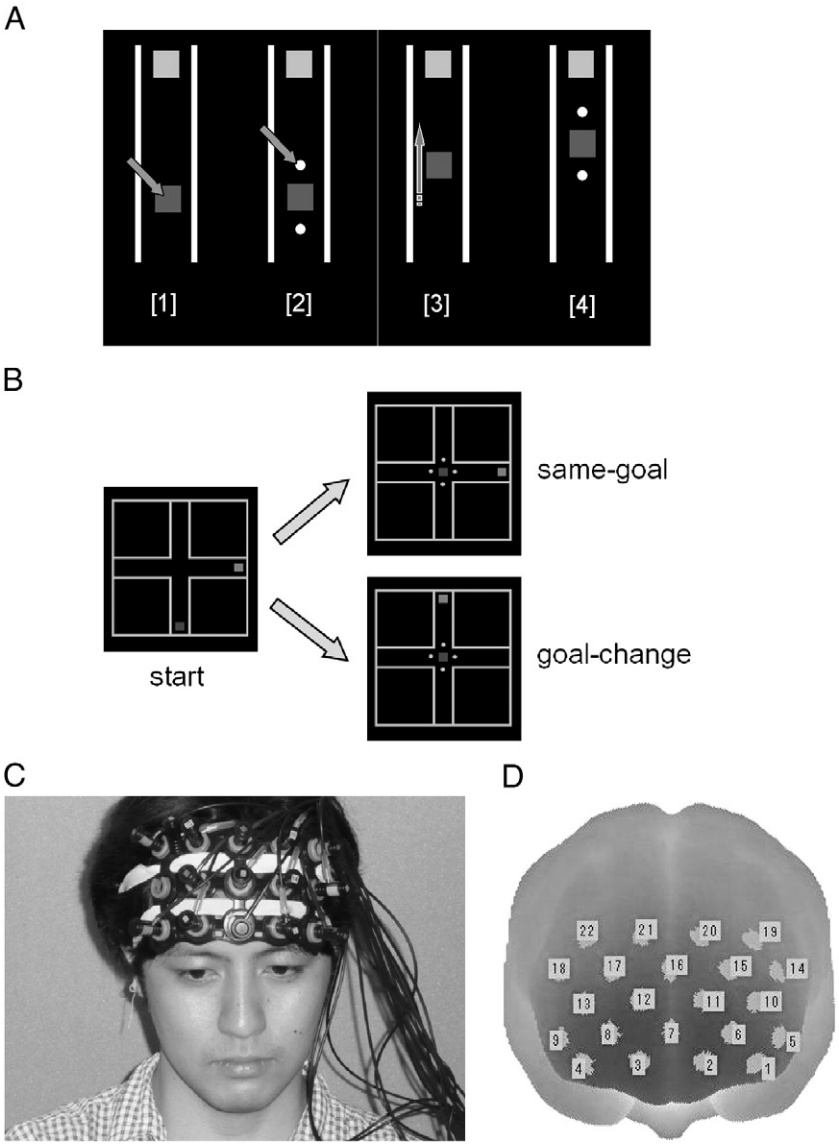

Fig. 1 – Tasks and setting. (A) Illustration of the target-moving task to move the target (red square; below) to the goal (blue square; above) in order to solve the maze on the touch screen. See the text for description of each target-moving stage, i.e., [1]-[4]. (B) The plus-shaped maze and the two conditions in the test session, i.e., same-goal and goal-change. (C) Placement of the NIRS measurement probe. A 3 × 5 optode array was positioned on the participants' foreheads. (D) Arrangement of measurement positions (22 channels). Locations of the channels were estimated by the method of virtual registration (Tsuzuki et al., 2007). The figure was drawn using the Platform for Optical Topography Analysis Tool (POTATo), developed by Advanced Research Laboratory, Hitachi, Ltd.

2.2. *NIRS results*

Channels with statistically significant oxy-Hb increase during the first and the second peak in contrast with the baseline period for each response type (i.e., same-correct, change-correct, change-error) are depicted in Fig. 3A. For the same-correct trials, a large number of the analyzed channels located at the bilateral prefrontal areas (especially middle frontal cortex but also superior and inferior frontal cortices) showed significant increases during the first peak $t=-6.242–2.272$, $ps<0.035$), while no significant hemodynamic changes occurred during the second peak ($t=-1.773–0.113$, $ps>0.094$). These data illustrate that during these trials oxy-Hb significantly increased 2–6 s after the start of the maze solution, followed by a return to the baseline level. The time course of Hb changes from several representative channels is consistent with these trends (Fig. 3B). For the change-correct trials, no significant changes in oxy-Hb across the participants were observed (first peak: $t=-2.376–0.038$, $ps>0.030$; second peak: $t=-0.003–2.940$, $ps>0.010$). For the change-error trials, a number of the channels (especially those located at right and medial superior-middle frontal cortices), though somewhat fewer than in the same-correct trials, showed significant increases in oxy-Hb during the first peak, similar to the same-correct

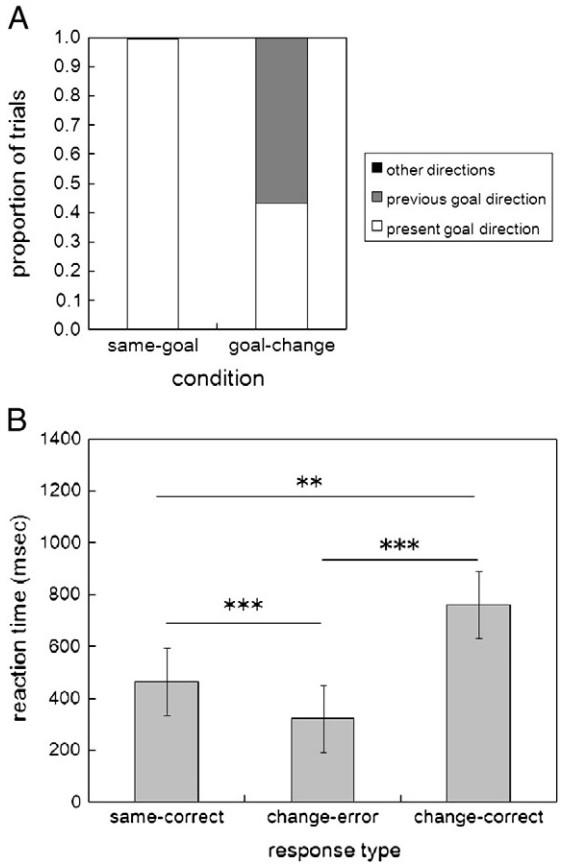

Fig. 2 – Behavioral results. (A) Proportions of the next movement directions of the target when it was at the center of the maze in the test session. "Present goal direction" shows trials in which directions of the next single movement when the target came to the center was correctly toward the present goal, i.e., the "fixed" goal in the same-goal condition and the goal after change of locations in the goal-change condition. "Previous goal direction" shows trials in the goal-change condition in which the direction of the movement right after the goal-shift was incorrectly toward the goal before change of locations. "Other directions" include three incorrect directions other than that toward the goal in the same-goal trials, whereas in the goal-change trials they include two incorrect directions other than those toward the previous (i.e., before change) or present (i.e., after change) goal. (B) Mean response time when the target was at the center of the maze in the test session, shown for each response type, i.e., same-correct, change-error and change-correct. The error bars indicate standard errors of the mean. $^{**}p<.01$; $^{***}p<.001$.

trials ($t=-5.249$–2.361, $ps<0.030$). In addition, during the second peak, a significant increase in oxy-Hb was found in the two channels of the right hemisphere, CH 4 ($t[18]=-3.545$, $p=0.0023$) and CH9 ($t[18]=-3.330$, $p=0.0037$). For the other channels, no significant increase in oxy-Hb was found during the second peak ($t=-2.532$–0.112, $p>0.021$). Anatomical labels (by Tzourio-Mazoyer et al., 2002) assigned to these significant channels were: CH4: orbital part of the middle frontal gyrus; CH9: inferior prefrontal cortex, according to the virtual registration method by Tsuzuki et al. (2007). Thus, in these trials, oxy-Hb significantly increased 2–6 s after the start of the maze solution similar to the same-correct trials, which was followed by an additional increase in oxy-Hb, especially in right anterior prefrontal areas. In many of the analyzed channels, patterns in hemodynamic changes having two peaks were observed, as depicted in Fig. 3B, as well as in Fig. 4, which shows changes in oxy-Hb for the change-error trials for all of the 18 analyzed channels.

To examine the hemispheric differences in hemodynamic changes for the two channels that showed significant increases in oxy-Hb during the second peak for the change-error trials, i.e., CHs 4 and 9, we directly compared these oxy-Hb changes with those in symmetrically located channels in the left hemisphere (CH1 and CH5, respectively). Specifically, a 2 × 3 two-way repeated-measures analysis of variance (ANOVA) with both hemisphere (right or left) and response type (same-correct, change-correct, or change-error) as within-subject factors was conducted for each channel pair. As to the comparison between CH4 (right) and CH1 (left), the main effect of hemisphere ($F[1, 2]=7.637$, $p=0.007$) and the main effect of response type ($F[1, 2]=16.478$, $p=0.000$) were significant, although the interaction between these two factors failed to reach statistical significance ($F[1, 2]=2.450$, $p=0.092$). Multiple comparison tests with Bonferroni correction revealed that increase in oxy-Hb for the change-error trials was significantly larger than that for the same-correct trials ($p=0.000$) or that for the change-correct trials ($p=0.000$), although there was no difference between same-correct and change-correct trials ($p=0.481$) (Fig. 4; see Fig. 5 as well). As to CH9 (right) and CH5 (left), the main effect of response type was significant ($F[1, 2]=14.399$, $p=0.000$), although the main effect of hemisphere ($F[1, 2]=0.681$, $p=0.411$) and the interaction between the two factors ($F[1, 2]=0.333$, $p=0.718$) failed to reach statistical significance. Multiple comparison tests with Bonferroni correction revealed that increases in oxy-Hb for the change-error trials was significantly larger than that for the same-correct trials ($p=0.000$) or that for the change-correct trials ($p=0.000$), although there was no difference between same-correct and change-correct trials ($p=0.335$). These results show that at least CH4 showed significantly greater increase in oxy-Hb after error responses than the counterpart in the left hemisphere. In addition, for all these channels the increase in oxy-Hb during the second peak was significantly greater in change-error trials than in the other response types.

We further explored the possible correlations between each participant's performance and the hemodynamic changes. Analysis of correlations between response time and increases in oxy-Hb revealed no statistically significant outcomes. We then analyzed correlations between the proportion of correct responses after the goal-shift and the increase in oxy-Hb during the first peak. With FDR correction, no channels (CHs 1–18) showed significant correlation between these factors in a channel by channel analysis, although some channels showed a tendency of negative correlation (e.g., same-correct trials; CH 13: R^2 $[N=20]=-0.488$, $p=0.015$, uncorrected). However, correlation between these factors was negative in 15 channels for the same-correct trials, 15 channels for the change-correct trials, and nine channels for the change-error trials. Therefore, as a next step a whole-channel analysis was conducted to examine correlation tendency in different conditions. Correlation coefficients (R^2) for the 18 channels were significantly below zero

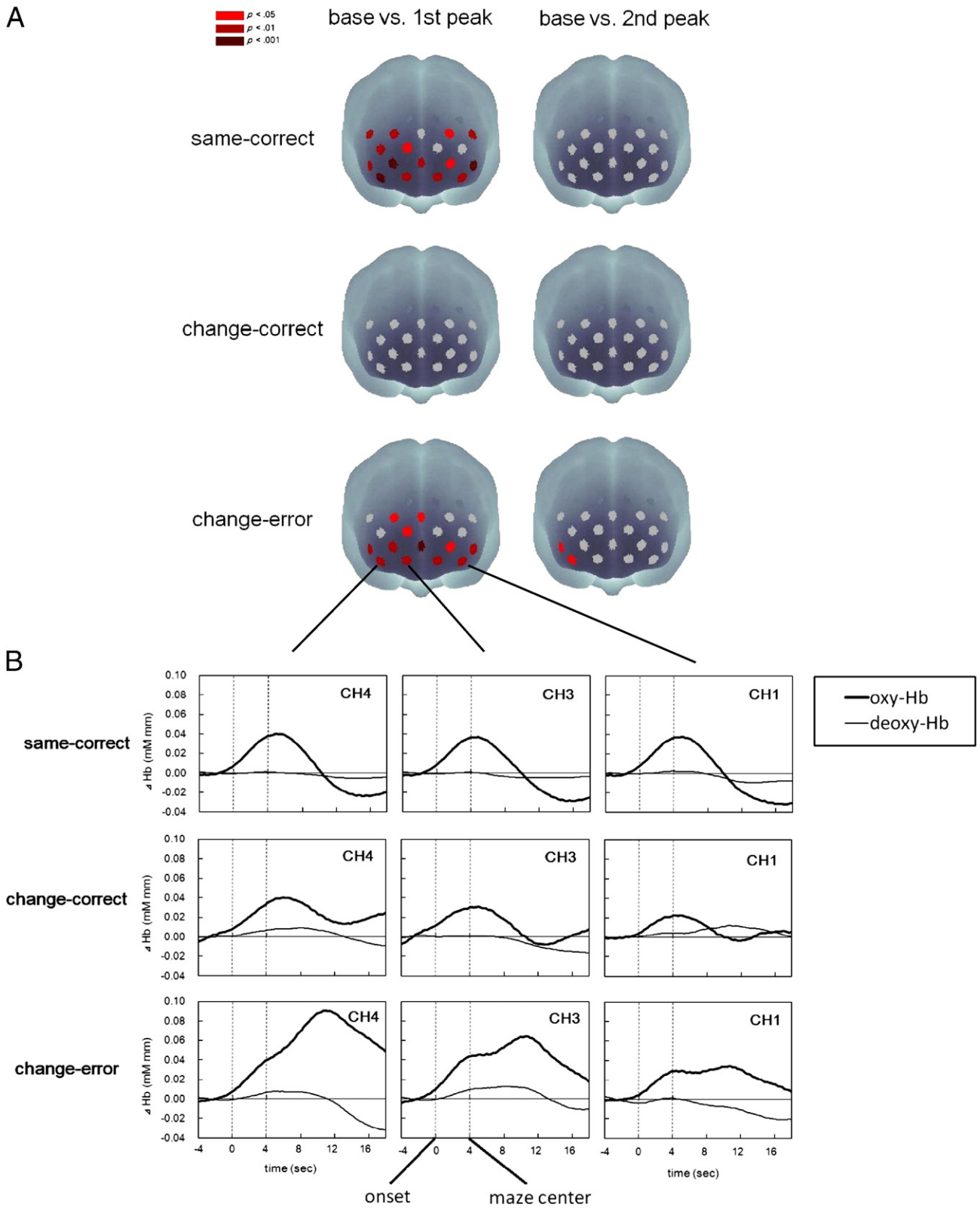

Fig. 3 – NIRS results. (A) Statistical p-maps of oxy-Hb increase during the first and the second peak in contrast with the baseline period, shown for each response type (i.e., same-correct, change-correct, change-error). Channels with significant oxy-Hb increase are marked with different red colors (FDR corrected $p<.05$, $p<.01$, and $p<.001$). The figure was drawn using POTATo. (B) Time course for signal changes of oxy- and deoxy-Hb in representative channels (CHs 1, 3, and 4), shown for each response type. The graphs represent the grand average of all participants. The dashed lines in each graph represent the moment the maze solution started and the moment the target reached the center of the maze, respectively.

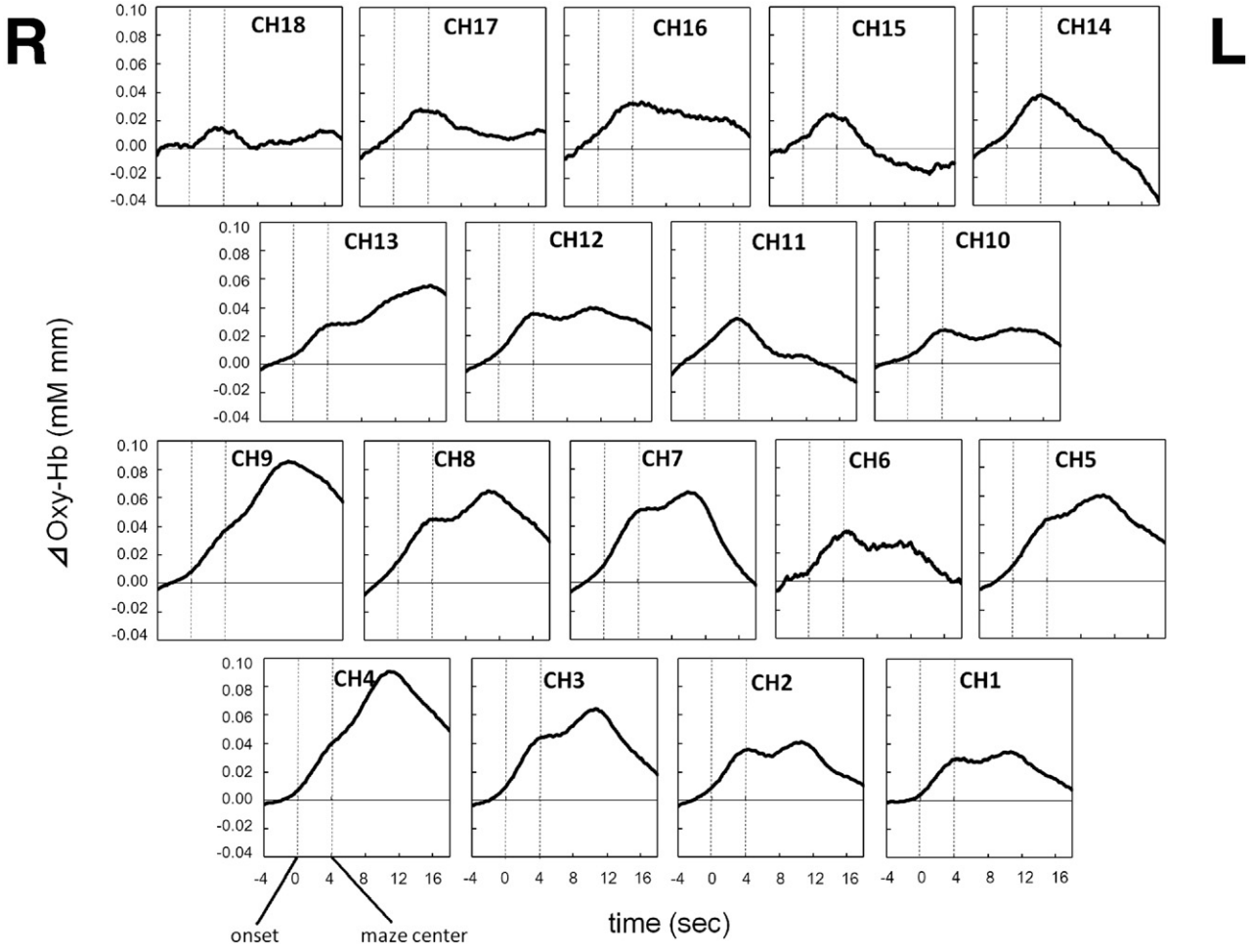

Fig. 4 – Time course for signal changes of oxy-Hb in change-error trials for all the analyzed channels (CHs 1–18), to show the hemodynamic change patterns having two peaks. The graphs represent the grand average of all participants. The dashed lines in each graph represent the moment the maze solution started and the moment the target reached the center of the maze, respectively.

for the same-correct (one-sample *t*-test; $t[17]=-5.231$, $p=0.000$) and the change-correct (one-sample *t*-test; $t[17]=-3.653$, $p=0.002$) trials, although they did not differ from zero for the change-error trials (one-sample *t*-test; $t[17]=0.351$, $p=0.730$). These correlations imply that participants who made relatively many errors immediately after the goal-shift tended to show greater increases in oxy-Hb when solving the tasks than those with fewer errors, at least for the same-correct and change-correct trials.

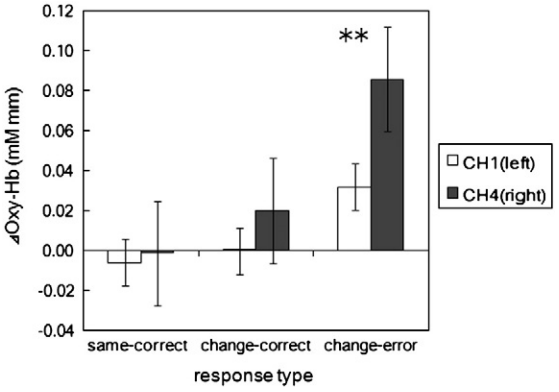

Fig. 5 – Oxy-Hb increase in CH4 and its counterpart in the left hemisphere, i.e., CH1, during the second peak in contrast with the baseline period, shown for each response type (i.e., same-correct, change-correct, change-error). Error bars indicate standard errors of the mean. $^{**}p < .01$.

3. Discussion

The present study using near-infrared spectroscopy examined prefrontal activation in adult humans performing a plus-shaped maze task presented on a touch screen that was previously used for pigeons and human children to assess planning processes. Adult humans in this study exhibited similar behavioral tendencies compared to avian subjects in previous studies, suggesting an analogy of problem solving in the behavioral level across species. Subjects frequently moved the target toward the previous goal location immediately after the goal jumped to another location when the target reached the center of the maze (i.e., change-error trials). This suggests planning *without* adjustment to change, as defined in the

introduction. Reaction time for this change-error case was shorter than those for the other response types, suggesting that these trials reflect cases when the plan for future movements was too strong to inhibit it without any careful consideration Also, in the trials in which subjects correctly moved the target toward the goal after the change in location (i.e., change-correct trials), reaction time at the center point was much longer than that in the other cases, which suggests planning *with* adjustment to change (i.e., better inhibition than the change-error case). The proportion of trials with correct adjustment was higher in the present study (43.3%) than in pigeons (30.6%; Miyata and Fujita, 2008) or in human children (13.5% for 3-year-olds and 38.3% for 4-year-olds; Miyata et al., 2009), despite the fact that we tried to increase the errors by presenting the tasks in pale colors while instructing the participants to solve them as quickly as possible. This seems to suggest that human adults employ higher-level planning including inhibition and flexible changing of behavior when confronted with unexpected events during the course of problem solving. Human adults seem to be superior in abilities for inhibition and flexibility from both evolutionary and developmental perspectives, which appear consistent with human adults' developed executive function of the frontal cortex.

The NIRS data collected during the maze task suggests different patterns of hemodynamic changes in the prefrontal area according to each behavioral pattern. In the baseline, same-correct trials, stable activation associated with task performance, i.e., increase in oxy-Hb concentration after the start of maze solution, was observed in wide areas of the prefrontal cortex from both hemispheres. This seems in agreement with the previous findings from neuroimaging studies suggesting that the prefrontal areas including the dorsolateral prefrontal cortex (DLPFC) are involved in human navigation (e.g., Moffat, 2009) as well as planning (e.g., van den Heuvel et al., 2003). A consistent trend was observed in the change-correct trials as well, although in these trials hemodynamic changes failed to reach statistical significance in any channels. On the other hand, in the change-error trials, relatively large increases in oxy-Hb were observed compared to other response types. Interestingly, in these trials concentration patterns having two peaks were observed in many channels, with the first peak in a similar manner as in the same-correct trials and the second peak found after the goal-shift (Fig. 3C).

These activation patterns may be interpreted in terms of planning for future moves, inhibition of such plans, or additional processes of reengagement into an alternative action following inhibition. That is, change-error trials seem to reflect the cases when planning for future movement toward the goal was dominant and inhibition of the plans failed to work immediately after the goal-shift. Thus, there could have been activation associated with planning in large areas of the prefrontal cortex, and a second increase in oxy-Hb. The latter may reflect use of additional cognitive resources required to adjust the direction of the target's movements after making incorrect responses. That is, after making errors toward the previous goal immediately after the goal-shift, subjects had to suppress further movement toward the incorrect direction and go back to the center of the maze to head for the new goal. This suppression and following reengagement after making errors may have required relatively large cognitive load. In contrast, change-correct trials seem to reflect cases when inhibition of the already planned actions immediately after the goal-shift was working relatively better than in the change-error trials. The successful inhibition followed by directing for a new goal without making errors may not have been cognitively demanding compared with the former change-error case. This seems to be consistent with the fact that no significant hemodynamic changes were observed in prefrontal cortex. In the baseline, same-correct trials, both of the cognitive components immediately after the goal-shift in the former two cases may have been intermixed in the participants' performance, which appears consistent with the fact that these trials showed stable hemodynamic changes associated with maze solution.

In the change-error trials, two channels in the right hemisphere, i.e., CHs 4 and 9, showed significant increases in oxy-Hb after the first peak. Lateralization was found in CH4 showing significantly larger activations compared with the corresponding channel in the left hemisphere (i.e., CH1). Although statistical significance for the second peak was obtained in only a limited number of channels compared with the first peak, it is noteworthy that channels located near the right inferior frontal cortex (IFC) showed the largest hemodynamic changes after the corrections of movement directions following errors. This localized activation is consistent with the previous findings from lesion, animal, and fMRI studies suggesting that the right IFC as well as the basal ganglia plays an important role in inhibitory control (e.g., Eagle and Robbins, 2003; Gauggel et al., 2004; Rubia et al., 2001). For example, in a recent fMRI study Boecker et al. (2011) used the stop-signal paradigm and showed that a similar neuronal network including primarily the right IFC was activated both when the participants suppressed an already initiated motor response and when that suppression was followed by a response reengagement into an alternative action. In the present maze task, the goal-change trials either required inhibition of already initiated sequential actions immediately after the goal-shift (i.e., change-correct) or inhibition of further incorrect responses toward the previous goal after making an error in order to go back to the center point (e.g., change-error). Both of these cases could include suppression of planned actions followed by reengagement into an alternative action. However, as mentioned above, the latter situation seems more cognitively demanding, which appears consistent with the present data showing statistically significant right IFC activation in change-error but not in change-correct trials. Beyond the previous fMRI studies, the present NIRS study with higher temporal resolution revealed the time course of brain activations for the two cognitive processes. Furthermore, the activation foci were different in those bimodal hemodynamic responses suggesting a cerebral network of the medial superior-middle frontal cortex to orbital part of the middle frontal cortex or the inferior prefrontal cortex for planning and inhibition/reengagement processes.

Another possible account for the right hemisphere superiority in the prefrontal activation found in this research concerns the fact that the task was visually based and not verbally mediated. That is, the hemispheric asymmetry found here may in part be due to the large involvement of visuo-spatial processes as opposed to linguistic or language-based thinking processes throughout the test period. Actually, there is a large body of evidence from working memory studies suggesting that verbal/

spatial systems are left/right lateralized, respectively (e.g., Reuter-Lorenz et al., 2000; Valler and Shallice, 1990). It thus seems quite interesting in the future quest to compare the differences of prefrontal activation patterns between the visual and verbal inhibition/planning tasks. While it is predictable that prefrontal function is involved in both these domains, there may be greater activation in the left PFC if the participants are required to use verbally guided plans. It is also promising to examine not only prefrontal but also parietal and temporal activation according the types of planning the participants use. These investigations are possible by using comparable settings as the present one, which potentially provides further effective use of the NIRS technique.

The present NIRS data suggest individual differences in prefrontal cortex activation while performing a maze planning task. Regarding the same-correct and change-correct trials, many channels showed negative correlations between the proportion of correct responses after the goal-shift and the increase in oxy-Hb during the first peak. For these two types of trials, correlation coefficients obtained from all the channels were significantly below zero. This may imply that the individuals who showed poorer inhibition of plans faced with the goal-shift needed greater cognitive resources when they showed such inhibitions compared with the individuals who showed more efficient adjustments. It appears that differences among participants may exist in the difficulty of the task, such that more or fewer cognitive resources are required. Further refined work in future with more participants may reveal stronger statistical support to this point.

To summarize, the present NIRS study showed that adult humans performed a computerized plus-shaped maze task with better inhibition and flexibility compared to pigeons and children, while showing hemodynamic changes characteristic of each response type. Particularly, our NIRS study clearly revealed the time course of two successive neurocognitive processes in relation to planning and inhibition/reengagement. Furthermore, activation depending on these two processes differed according to behavioral patterns and brain regions. We also confirmed the relevance of NIRS to examine regional brain activation in a natural problem solving situation using a touch-sensitive screen (see also Miyata et al., in press). Because this non-invasive technique can be used not only for adults but also for infants and young children (e.g., Minagawa-Kawai et al., 2009), it would be useful to explore the developmental course of maze solution and planning at the neuronal level. Also, by using similar maze tasks, it would be possible to explore the neuronal bases of spatial problem solving and planning in non-human species, including birds. These works from both developmental and comparative perspectives may shed light on the origins of planning and problem solving from a neurological perspective.

4. Experimental procedures

4.1. *Participants*

Twenty healthy Japanese adults (13 females and 7 males; age, 20–33 years; mean age = 23.3 years, *SD* = 3.0) participated in this experiment. The participants had normal or corrected-to-normal visual acuity. Handedness of the participants was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), which revealed that all except for one male (24 years) were right-handed. The sole left-handed participant was included in the analysis because his NIRS data was consistent with trends revealed in the other 19 participants. This study was approved by the Ethics Committee of Keio University (no. 09037-3).

4.2. *Materials*

We used computer-generated stimuli composed of an outer frame, a target, a goal, guides (small dots), and a border forming a cross. The entire task was presented within a square area (550 × 550 pixels: about 14.5 × 14.5 cm), with 10-pixel-wide gray lines forming the outer frame. The target was a small pale red square (20 × 20 pixels: about 5 × 5 mm), around which four small gray dots (8 pixels in diameter) appeared as the "guides". The goal was a pale blue square of the same size as the target. The border was a 10-pixel-wide gray line surrounding the plus-shaped area within the outer frame. Pale, instead of bright, colors were used to increase task difficulty, which was expected to yield more incorrect responses after the goal-shift. (See the Procedure section to learn how each of these materials was used in the experiment.)

4.3. *Procedure*

The experiment was conducted in a dim, sound-attenuated room, where the participants were seated in a comfortable chair. A 46-cm (18.1 in.) TFT LCD monitor with a built-in Ultrasonic Surface-Wave touch screen (AS4641D, Iiyama, Tokyo, Japan) was located on a table in front of the participant, who solved the maze tasks by making sequential touches to the monitor with his or her fingers. NIRS recording was conducted during a test session in which the participant solved a plus-shaped maze task. The program for the behavioral task was written in Microsoft VisualBasic 6.0.

4.3.1. *Behavioral task*

We used the same planning task that was previously used for pigeons (Miyata et al., 2006; Miyata and Fujita, 2008, 2010) and human children (Miyata et al., 2009). As illustrated in Fig. 1A, the task was to move the target (a red square; the one below in this illustration) to the goal (a blue square; the one above) in order to solve the maze on the computer screen. To move the target, participants had to touch the target first at the beginning of each trial (**[1]**), which resulted in small white dots (i.e., the guides) appearing at four locations—above, below, right, and left—surrounding the target. No guides appeared beyond the thick gray line, which represented a "border" (**[2]**). When the participants touched one guide, all guides disappeared and the target moved 60 pixels in the direction of the touched guide in 0.6 s (**[3]**), followed by reappearance of the guides (**[4]**). Thus, the participants could freely move the target in multiple directions on the touch screen, but with the exception that they could not move it beyond the white lines ("borders") because no guides appeared beyond the borders. Participants were required to move the target each time by touching one of the available guides, until the target came to the location of the goal.

Participants were trained for three trials on the simple target-moving task, which had no borders and in which subjects had to move the target six times along a straight line to the goal (i.e., either above→below, below→above, right→left, or left→right). This was followed by the test session with a plus-shaped maze (Fig. 1B). The test session required the participants to move the target, located at the end of one arm, toward the goal, located at another, by touching one of the guides surrounding it. The end of each arm was four movements away from the center point. The participants were able to move the target only within the plus-shaped area because there were no guides beyond the border. All four guides appeared at a time only when the target was at the center of the maze. The stimulus maze appeared after a 10-s inter-trial interval, during which a blank display was presented and the participants were told to wait. Successful moving of the target to the goal immediately led to the next inter-trial interval. The test session consisted of 36 trials: 30 baseline trials in the same-goal condition and six test trials in the goal-change condition (Fig. 1B). In the same-goal condition, the 12 possible combinations of the target-goal locations appeared equally often, with no change in the goal location within each trial. In the goal-change condition, the goal suddenly jumped to the end of one of the two remaining arms when the target reached the center of the maze. The goal-change patterns differed in each trial and were pseudo-randomized. The number of the goal-change trials was limited to six in order to obtain both incorrect (i.e., change-error) and correct (i.e., change-error) trials equally often: Actually, our preliminary investigation revealed that, with more experience of the goal-shift human participants were quickly habituated to these events and tended to make fewer and fewer errors. During the test session, participants were instructed to solve the task as quickly as possible by using efficient maze-solving strategies. Participants had to move their fingers but were told not to move their head or speak, to reduce motion artifacts, unless they wanted to terminate the session.

4.3.2. *NIRS measurement*

During the test session, hemodynamic changes in prefrontal areas were measured using NIRS (ETG7000, Hitachi Medical Corporation, Tokyo, Japan). With this instrument, changes in hemoglobin (Hb) concentration and its oxygenation level accompanying regional brain activities can be noninvasively measured by emitting and detecting continuous near-infrared lasers with two wavelengths. The system had eight near-infrared light sources and seven detectors, which were arrayed in a 3 × 5 lattice pattern and were embedded in a soft silicon holder to fit participants' foreheads (Fig. 1C). This configuration formed 22 measurement points, i.e., "channels," corresponding to each source-detector pair (Fig. 1D). A method of virtual registration was applied (Tsuzuki et al., 2007). This method estimated the coordinates of the optodes and channels in the Montreal Neurological Institute (MNI) space, and based on that coordinate, brain regions were estimated using automated anatomical labeling (AAL) (Tzourio-Mazoyer et al., 2002). Specifically, the holder was placed so that the center optode on the lowest row, i.e., the primary reference optode, aligns with Fpz and the five optodes in the lowest row, i.e., the secondary reference optodes, are aligned with the horizontal reference curve (T3-Fpz-T4 line) on the scalp in a balanced manner, according to the international 10–20 system.

4.4. *Data processing*

The concentrations of oxygenated and deoxygenated Hb were calculated from the absorbance changes of 780- and 830-mm laser beams sampled at 10 Hz. After the removal of inappropriately fitted channels and trials with artifacts, the data were smoothed with a 5-s moving average. Data from channels on the highest row (CHs 19–22) were excluded from the subsequent analysis, because of their relatively noisy signals due to failure of good fit between the probe and the skin. For the same-correct trials, the averaged data of the first six trials for each participant were used. For the change-correct and change-error trials, Hb data were either averaged across two to six trials or from a single trial for each participant. Hb data for the maze solution period were then normalized with a 5-s baseline period just before the onset of the maze solution, which was determined 4 s before the moment the target reached the center point (mean duration from the start to the center was 4.0 s). The response peaks for each response type were evaluated. Because one peak in oxy-Hb was observed within 3.5–4.2 s after the onset of the maze solution for each response type, averaged data of 2–6 s were used as the first analysis window. A second peak in oxy-Hb was also observed 10.5 s after the onset of the maze solution for the change-error trials, and thus averaged data of 8.5–12.5 s were used as the second analysis window.

To create a statistical map containing the 18 analyzed channels, we used a false discovery rate (FDR) method to correct multiple comparisons. In this method, the expected proportions of false positive channels among declared *significant* channels were controlled. We set the threshold at the FDRs of $p < .05$, $p < .01$, and $p < .001$, so that no more than 5%, 1%, and 0.1% of channels were false positives on the average (Singh and Dan, 2006).

Acknowledgments

Funding for this study was provided by the Research Fellowship of the Japan Society for the Promotion of Science (JSPS) for Young Scientists to Hiromitsu Miyata, and by the Japan Ministry of Education, Culture, Sport, Science, and Technology (MEXT) Global COE Program, D-09, to Keio University, Japan.

REFERENCES

Antonova, E., Parslow, D., Brammer, M., Dawson, G.R., Jackson, S.H., Morris, R.G., 2009. Age-related neural activity during allocentric spatial memory. Memory 17, 125–143.

Baker, S.C., Rogers, R.D., Owen, A.M., Frith, C.D., Dolan, R.J., Frackowiak, R.S., Robbins, T.W., 1996. Neural systems engaged by planning: a PET study of the Tower of London task. Neuropsychologia 34, 515–526.

Biro, D., Matsuzawa, T., 1999. Numerical ordering in a chimpanzee (*Pan troglodytes*): planning, executing, and monitoring. J. Comp. Psychol. 113, 178–185.

Boecker, M., Drueke, B., Vorhold, V., Knops, A., Philippen, B., Gauggel, S., 2011. When response inhibition is followed by response reengagement: An event-related fMRI study. Hum. Brain Mapp. 32, 94–106.
Correia, S.P.C., Dickinson, A., Clayton, N.S., 2007. Western scrub-jays (*Aphelocoma californica*) anticipate future needs independently of their current motivational state. Curr. Biol. 17, 856–861.
Dagher, A., Owen, A.M., Boecker, H., Brooks, D.J., 1999. Mapping the network for planning: a correlational PET activation study with the Tower of London task. Brain 122, 1973–1987.
Dehaene, S., Changeux, J.P., 1997. A hierarchical neuronal network model for planning behavior. Proc. Natl Acad. Sci. USA 94, 13293–13298.
Eagle, D.M., Robbins, T.W., 2003. Inhibitory control in rats performing a stop-signal reaction-time task: effects of lesions of the medial striatum and d-amphetamine. Behav. Neurosci. 117, 1302–1317.
Emery, N.J., Clayton, N.S., 2001. Effects of experience and social context on prospective caching strategies in scrub jays. Nature 414, 443–446.
Folley, B.S., Astur, R., Jagannathan, K., Calhoun, V.D., Pearlson, G.D., 2010. Anomalous neural circuit function in schizophrenia during a virtual Morris water task. Neuroimage 49, 3373–3384.
Fragaszy, D., Johnson-Pynn, E., Hirsh, E., Brakke, K., 2003. Strategic navigation of two-dimensional alley mazes: comparing capuchin monkeys and chimpanzees. Anim. Cogn. 6, 149–160.
Gauggel, S., Rieger, M., Feghoff, T.A., 2004. Inhibition of ongoing responses in patients with Parkinson's disease. J. Neurol. Neurosurg. Psychiatry 75, 539–544.
Ghatan, P.H., Hsieh, J.C., Wirsen-Méurling, A., Wredling, R., Eriksson, L., Stone-Elander, S., Levander, S., Ingvar, M., 1995. Brain activation induced by the perceptual maze test: a PET study of cognitive performance. Neuroimage 2, 112–124.
Iaria, G., Palermo, L., Committeri, G., Barton, J.J., 2009. Age differences in the formation and use of cognitive maps. Behav. Brain Res. 196, 187–191.
Iversen, I.H., Matsuzawa, T., 2003. Development of interception of moving targets by chimpanzees (*Pantroglodytes*) in an automated task. Anim. Cogn. 6, 169–183.
Kawai, N., Matsuzawa, T., 2000. Numerical memory span in a chimpanzee. Nature 403, 39–40.
Maki, A., Yamashita, Y., Ito, Y., Watanabe, E., Mayanagi, Y., Koizumi, H., 1995. Spatial and temporal analysis of human motor activity using noninvasive NIR topography. Med. Phys. 22, 1997–2005.
Minagawa-Kawai, Y., Naoi, N., Kojima, S., 2009. A new approach to functional neuroimaging: near-infrared spectroscopy (NIRS). Center for Advanced Research on Logic and Sensibility (CARLS), Keio University, Japan.
Miyata, H., Fujita, K., 2008. Pigeons (*Columba livia*) plan future moves on computerized maze tasks. Anim. Cogn. 11, 505–516.
Miyata, H., Fujita, K., 2010. Route selection by pigeons (*Columba livia*) in "traveling salesperson" navigation tasks presented on an LCD screen. J. Comp. Psychol. 124, 433–446.
Miyata, H., Ushitani, T., Adachi, I., Fujita, K., 2006. Performance of pigeons (*Columba livia*) on maze problems presented on the LCD screen: In search for preplanning ability in an avian species. J. Comp. Psychol. 120, 358–366.
Miyata, H., Itakura, S., Fujita, K., 2009. Planning in human children (*Homo sapiens*) assessed by maze problems on the touch screen. J. Comp. Psychol. 123, 69–78.
Miyata, H., Gajdon, G.K., Huber, L., Fujita, K., 2011. How do keas (*Nestor notabilis*) solve artificial-fruit problems with multiple locks ? Anim. Cogn. 14, 45–58.
Miyata, H., Watanabe, S. & Minagawa-Kawai, Y., in press. Prefrontal activation during and before solution of an eight-arm shuriken-shaped maze task presented on a touch screen: A near-infrared spectroscopy study. Inquiries into humans and societies. Studies in sociology, psychology and education.
Moffat, S.D., 2009. Aging and navigation: what do we know and where do we go? Neuropsychol. Rev. 19, 478–489.
Moffat, S.D., Elkins, W., Resnick, S.M., 2006. Age differences in the neural systems supporting human allocentric spatial navigation. Neurobiol. Aging 22 787-965-972.
Mulcahy, N.J., Call, J., 2006. Apes save tools for future use. Science 312, 1038–1040.
Mushiake, H., Saito, N., Sakamoto, K., Itoyama, Y., Tanji, J., 2006. Activity in the prefrontal cortex reflects multiple steps of future events in action plans. Neuron 50, 631–641.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9, 97–113.
Owen, A.M., 1997. Cognitive planning in humans: neuropsychological, neuroanatomical and neuropharmacological perspectives. Prog. Neurobiol. 53, 431–450.
Pantelis, C., Barnes, T.R., Nelson, H.E., Tanner, S., Weatherley, L., Owen, A.M., Robbins, T.W., 1997. Frontal-striatal cognitive deficits in patients with chronic schizophrenia. Brain 120, 1823–1843.
Raby, C.R., Alexis, D.M., Dickinson, A., Clayton, N.S., 2007. Planning for the future by western scrub-jays. Nature 445, 919–921.
Reuter-Lorenz, P.A., Jonides, J., Smith, E.E., Hartley, A., Miller, A., Marshuetz, C., Koeppe, R.A., 2000. Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. J. Cogn. Neurosci. 12, 174–187.
Robbins, T.W., 1998. Dissociating executive functions of the prefrontal cortex. In: Roberts, T.W., Weiskrantz, L. (Eds.), The Prefrontal Cortex. Executive and Cognitive Functions. Oxford Univ. Press, Oxford.
Rubia, K., Russell, T., Overmeyer, S., Brammer, M.J., Bullmore, E.T., Sharma, T., Simmons, A., Williams, S.C., Giampietro, V., Andrew, C.M., Taylor, E., 2001. Mapping motor inhibition: Conjunctive brain activations across different versions of go/no-go and stop tasks. Neuroimage 13, 250–261.
Shallice, T., 1982. Specific impairments of planning. Philos. Trans. R. Soc. Lond. B Biol. Sci. 298, 199–209.
Shima, K., Isoda, M., Mushiake, H., Tanji, J., 2007. Categorization of behavioural sequences in the prefrontal cortex. Nature 445, 315–318.
Singh, A.K., Dan, I., 2006. Exploring the false discovery rate in multichannel NIRS. Neuroimage 33, 542–549.
Suddendorf, T., Corballis, M.C., 1997. Mental time travel and the evolution of the human mind. Genet. Soc. Gen. Psychol. Monogr. 123, 133–167.
Tsuzuki, D., Jurcak, V., Singh, A.K., Okamoto, M., Watanabe, E., Dan, I., 2007. Virtual spatial registration of stand-alone fNIRS data to MNI space. Neuroimage 34, 1506–1518.
Tulving, E., 1983. Elements of episodic memory. Clarendon Press, Oxford, England.
Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15, 273–289.
Valler, G., Shallice, T., 1990. Neuropsychological impairments of short term memory. Cambridge University Press, Cambridge.
van den Heuvel, O.A., Groenewegen, H.J., Barkhof, F., Lazeron, R.H.C., van Dyck, R., Veltman, D.J., 2003. Frontostriatal system in planning complexity: a parametric functional magnetic resonance version of Tower of London task. Neuroimage 18, 367–374.
Veale, D.M., Sahakian, B.J., Owen, A.M., Marks, I.M., 1996. Specific cognitive deficits in tests sensitive to frontal lobe dysfunction in obsessive-compulsive disorder. Psychol. Med. 26, 1261–1269.