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Abstract	The present study using near-infrared spectroscopy (NIRS) examined prefrontal activation associated with maze-solving performance and preplanning in adult humans. The participants were required to solve an eight-arm shuriken-shaped maze, comparable to the one used for pigeons to behaviorally assess preplanning, by moving a target square to a goal square presented on a touch-sensitive screen. The maze-solution phase was preceded by a 10-s preview phase during which the participants could observe but were not allowed to solve the maze. The participants, in contrast with pigeons, made few incorrect responses in trials in which the goal jumped to the end of another arm following the preview phase. The NIRS data revealed two-peak waveforms, with the first peak during the preview phase and the second one during the solution phase, most evidently in baseline trials. Significant increase in oxy-Hb was found near right dorsolateral prefrontal cortex (DLPFC) during the solution phase, while hemodynamic changes during the preview phase failed to reach statistical significance. The data suggest that, although human adults may have planned the solution of the maze during the preview phase, they needed to employ relatively small amount of cognitive resources throughout this task. Developmental and comparative perspectives for investigating neural correlates of preplanning are discussed.
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近赤外線分光法による検討

Prefrontal Activation During and Before Solution of an Eight-Arm
Shuriken-Shaped Maze Task Presented on a Touch Screen:
A Near-Infrared Spectroscopy Study

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The present study using near-infrared spectroscopy (NIRS) examined prefrontal activation associated with maze-solving performance and preplanning in adult humans. The participants were required to solve an eight-arm shuriken-shaped maze, comparable to the one used for pigeons to behaviorally assess preplanning, by moving a target square to a goal square presented on a touch-sensitive screen. The maze-solution phase was preceded by a 10-s preview phase during which the participants could observe but were not allowed to solve the maze. The participants, in contrast with pigeons, made few incorrect responses in trials in which the goal jumped to the end of another arm following the preview phase. The NIRS data revealed two-peak waveforms, with the first peak during the preview phase and the second one during the solution phase, most evidently in baseline trials. Significant increase in oxy-Hb was found near right dorsolateral prefrontal cortex (DLPFC) during the solution phase, while hemodynamic changes during the preview phase failed to reach statistical significance. The data suggest that, although human adults may have planned the solution of the maze during the preview phase, they needed to employ relatively small amount of cognitive resources throughout this task. Developmental and comparative perspectives for investigating neural correlates of preplanning are discussed.

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 in-

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creased, 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 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; Frigaszy 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., 2010) 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) used a plus-shaped maze and its variation, i.e., an eight-arm *shuriken* (a Japanese traditional throwing knife)-shaped maze task, and 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 navigation or immediately after the preview phase (see also Miyata and Fujita, 2010). We also modified these detour and plus-shaped 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 before and during solution of a problem in adult humans. We used an eight-arm *shuriken*-shaped maze task presented on a touch screen previously used to test 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 visuospatial 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. Miyata et al. (submitted) previously applied the plus-shaped maze on the touch screen to measure prefrontal activation with NIRS. They showed human adults' better behavioral inhibition than pigeons/children. They also found hemodynamic changes having two peaks especially near the right inferior frontal cortex (IFC). This IFC activation suggested use of additional cognitive resources for inhibition and reengagement after making errors, consistently with the previous findings from lesion, animal, and fMRI studies (e.g., Boecker et al., 2010; Eagle and Robbins, 2003; Gauggel et al., 2004; Rubia et al., 2001). The present *shuriken*-shaped maze task had a 10-s preview (prior observation) period before the start of solution. This allows examination of neuronal activation associated with planning not only during but also before solution of a problem.

The aim of the present NIRS study was to evaluate prefrontal activation associated with planning using a computerized *shuriken*-shaped maze task. As in the previous study with pigeons (Miyata and Fujita, 2008), 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 goal-change 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. In addition, we also introduced a condition in which no goal appeared during the preview phase. Because participants in this condition could not plan future actions during the preview phase, we expected to observe no prefrontal activation during the preview phase.

METHODS

Participants

Twenty healthy Japanese adults (13 females and 7 males; age, 20–33 years; mean age=23.3 years, $SD=3.1$) 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).

Stimuli

We used computer-generated stimuli composed of an outer frame, a target, a goal, guides (small

dots), and a border forming the maze. 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 *shuriken*-shaped area within the outer frame (A *shuriken* is a Japanese traditional throwing knife typically used by *ninjas*). Pale, instead of bright, colors were used for the maze-solution phase to increase task difficulty, which was expected to yield more incorrect responses after the goal-shift. In contrast, for the preview display we used the outer frame, the target, the goal, the guides and the border presented in bright colors (See the Procedure section to learn how each of these materials was used in the experiment.)

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 inches) 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 navigation and 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 *shuriken*-shaped maze task. The program for the behavioral task was written in Microsoft VisualBasic 6.0.

Behavioral Task

We used the same navigation task that was previously used for pigeons (Miyata et al., 2006; Miyata and Fujita, 2008; Miyata and Fujita, 2010) and human children (Miyata et al., 2009). As illustrated in Figure 1(A), 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 gray 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 navigation 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 *shuriken*-shaped maze (Figure 1[B]). The test session required the participants to move the target, located at the center of the maze, toward the goal, located at the end of one arm, by touching one of

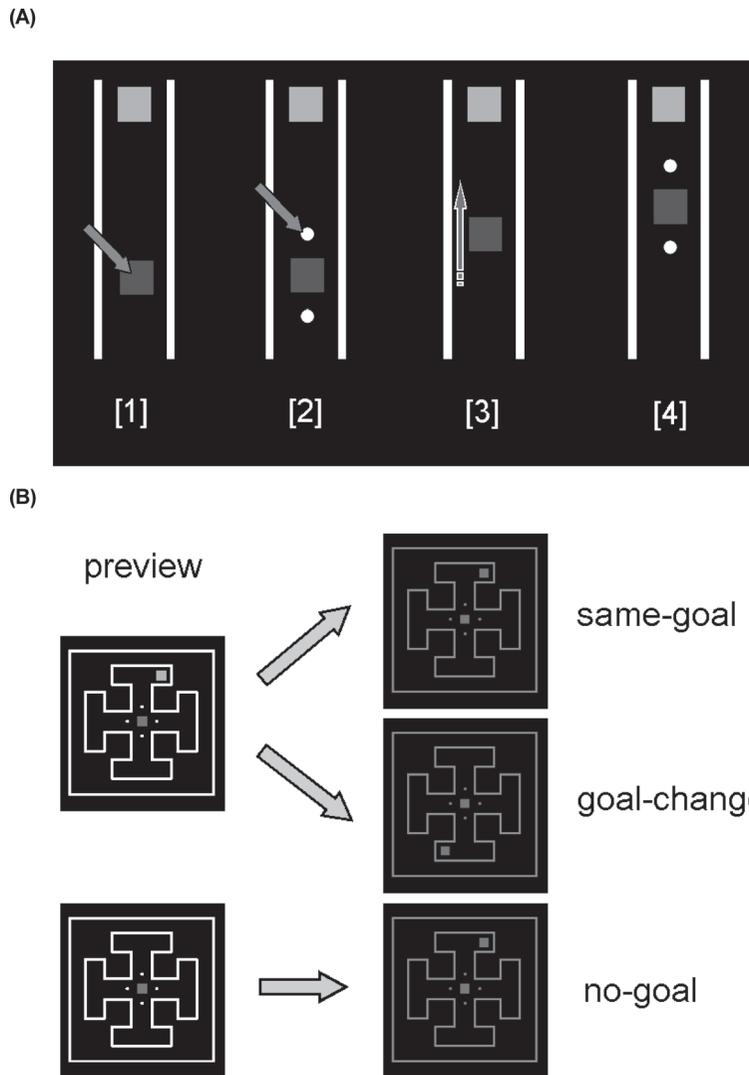


Figure 1. Behavioral task. (A) Illustration of the navigation task to move the target (red square; below) to the goal (blue square; above) in order to solve the maze on the touch screen. See the text for description of each navigation stage, i.e., [1]-[4]. (B) The eight-arm *shuriken*-shaped maze and the three conditions in the test session, i.e., same-goal, goal-change, and no-goal.

the guides surrounding it. The end of each arm was four movements away from the starting point. The participants were able to move the target only within the *shuriken*-shaped area because there were no guides beyond the border. All four guides appeared at a time only when the target was at the starting point. After a 10-s inter-trial interval with a blank display, the preview maze appeared in bright colors for 10-s, during which participants were instructed to wait by planning the solution of the maze. The color of the maze then turned pale, when participants were allowed to start by

touching the guide (participants did not need to touch the target at the beginning of each trial). Successful navigation of the target to the goal immediately led to the next inter-trial interval. The test session consisted of 24 trials: ten baseline trials in the same-goal condition, six trials in the goal-change condition, and eight trials in the no-goal condition (Figure 1[B]). In the same-goal condition, the goal appeared at one end of the eight arms equally often, with no change in the goal location within each trial. In the goal-change condition, the goal location changed the moment the color of the display became pale from the preview to the solution phase (before the participant's response to the solution display). The goal-change patterns differed in each trial and were pseudo-randomized. All the trials in the goal-change condition caused change in the correct directions of the first movement right after change of goal locations. The no-goal condition was the same as the same-goal condition except that no goal appeared during the preview phase. During the solution phase of 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.

NIRS Measurement

During the test session, hemodynamic changes in prefrontal areas were measured using NIRS (ETG-7000, 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 (Figure 2[A]). This configuration formed 22 measurement points, i.e., "channels", corresponding to each source-detector pair (Figure 2[B]). A method of virtual registration was applied (Tsunami 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.

Data Processing

The concentrations of oxygenated and deoxygenated Hb were calculated from the absorbance changes of 780- and 830-nm 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, change-correct, and the no-goal trials respectively, the averaged data of the first six trials for each participant were used. Only two participants (a male, 24 years; a male, 21 years) started

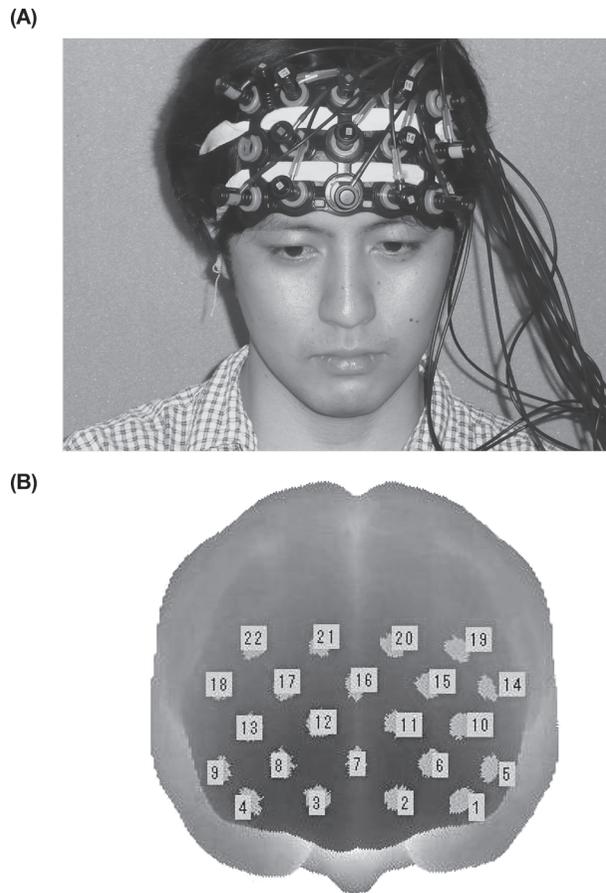


Figure 2. NIRS probe setting. (A) Placement of the NIRS measurement probe. A 3×5 optode array was positioned on the participants' foreheads. (B) Arrangement of measurement positions (22 channels). Locations of the channels were estimated by the method of virtual registration (Tsuzuki et al., 2007). The figure was drawn using the Platform for Optical Topography Analysis Tool (POTATo), developed by Advanced Research Laboratory, Hitachi, Ltd.

by making errors toward the previous goal location in one goal-change trial, which were excluded from analysis. Hb data for the preview and the maze-solution phases were then normalized with a 5-s baseline period just before the start of the preview phase. The response peaks for each response type were evaluated. Because one peak in oxyHb was observed within 4.5–6.0 s after the start of the preview phase for each response type, averaged data of 3–7 s were used as the first analysis window. A second peak in oxyHb was also observed 15.0–16.5 s after the start of the preview phase, and thus averaged data of 13–17 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 $p < .05$, so that no more than 5% of channels were false positives on the average (Singh and Dan, 2006). We also considered another threshold at the FDRs of $p < .06$, in order to reveal channels that approached significance.

RESULTS

Behavioral Results

Analysis was done for the 24 test trials, in comparable ways as described by Miyata and Fujita (2008). Figure 3(A) shows the proportions of the first movement directions of the target for the same-goal and the goal-change trials. Proportions of correct responses accounted for 99.5% of the same-goal trials and 98.3% of the goal-change trials, with no significant differences between these conditions (Wilcoxon signed-rank test; $Z [N=20] = -1.089$; $p = .276$). Thus, the participants made few incorrect responses immediately after the goal jumped to another end of the arm in the goal-change condition, which resulted in as accurate performance in the goal-change as that in the same-goal condition.

Figure 3(B) shows first response time (latency of response), that is, latency between the moment when the color of the maze display became pale after the preview phase and the moment when the first touch to the guide dot was made for the movement. Movements toward "other directions" (1 trial in the same-goal condition) and "previous goal direction" (2 trials in the goal-change condition) were excluded from analysis. The remaining trials divided into the following three response types were then analyzed: correct movements in the same-goal and the goal-change condition (i.e., same-correct and change-correct, respectively), and the no-goal trials. A one-way repeated-measures ANOVA failed to reveal a significant effect of response type ($F[2, 38] = 1.149$, $p = .328$). Multiple comparison tests with Bonferroni correction showed a trend toward longer response time in the no-goal than in the same-correct trials ($p = .074$), although for the other pairs differences were insignificant (same-correct and change-correct: $p = .571$; no-goal and change-correct: $p = 1.000$). These data show that participants started to react to the maze-solution display with equal quickness in all these response types, even though they started somewhat more slowly in the no-goal trials compared with the baseline, same-correct trials.

NIRS Results

Channels with statistically significant oxy-Hb increase during the preview and the solution phase in contrast with the baseline period for the same-correct trials are depicted in Figure 4(A). No significant hemodynamic changes occurred during the preview phase ($t = -1.945$ to -0.363 , $p_s > 0.05$). During the solution phase, a significant increase in oxy-Hb was found in the two channels of the right hemisphere, CH13 ($t[19] = -3.564$, $p = 0.002$) and CH17 ($t[18] = -3.649$, $p = 0.002$). Oxy-Hb increase in the other two channels of the right hemisphere, CH8 ($t[19] = -2.889$, $p = 0.009$) and CH18 ($t[18] = -2.814$, $p = 0.011$), also approached significance. For the other channels, no significant increase in oxy-Hb was found during the second peak ($t = -2.438$ to -1.282 , $p_s > 0.02$). Anatomical labels (by Tzourio-Mazoyer et al., 2002) assigned to these significant / marginally significant channels were: CHs 8 and 17: superior frontal

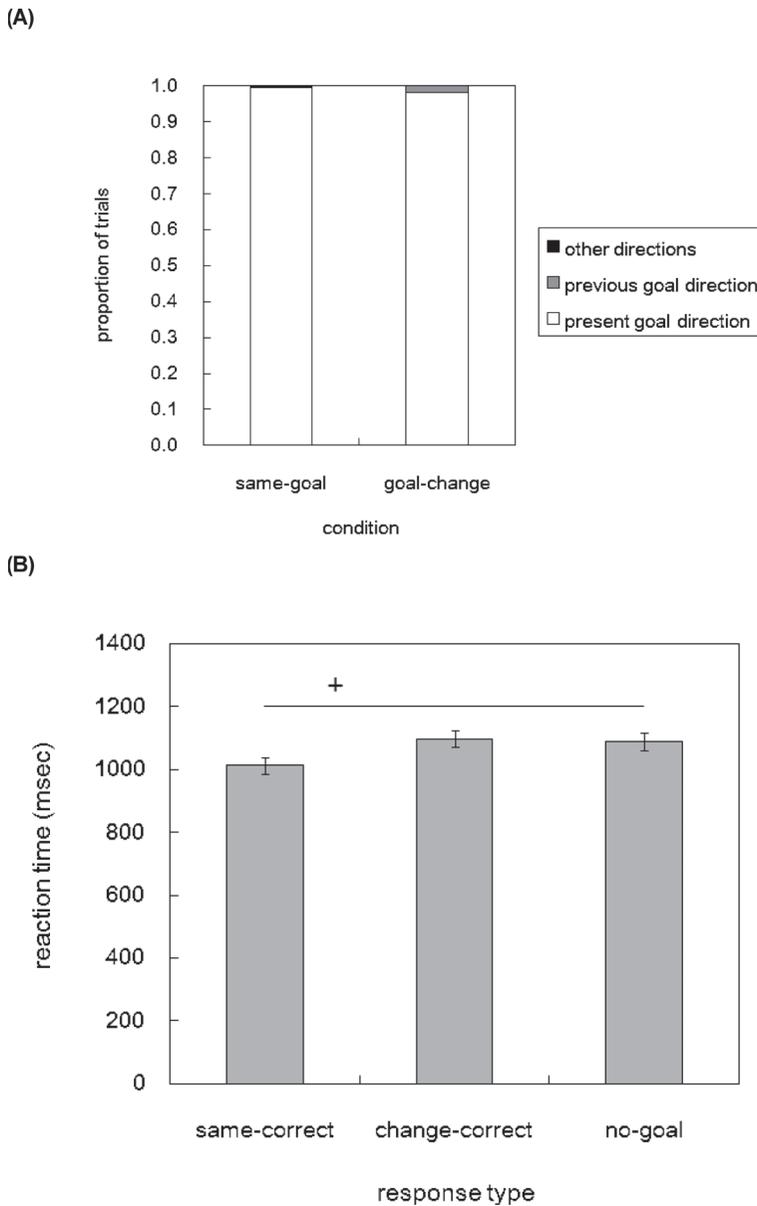


Figure 3. Behavioral results. (A) Proportions of the first movement directions of the target for the same-goal and goal-change conditions in the test session. “Present goal direction” shows trials in which directions of the first movement was correctly toward the present goal, i.e., the “fixed” goal 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 first response time in the test session, shown for the three response types, i.e., same-correct, change-correct, and no-goal. The error bars indicate standard errors of the mean. $+p < .10$.

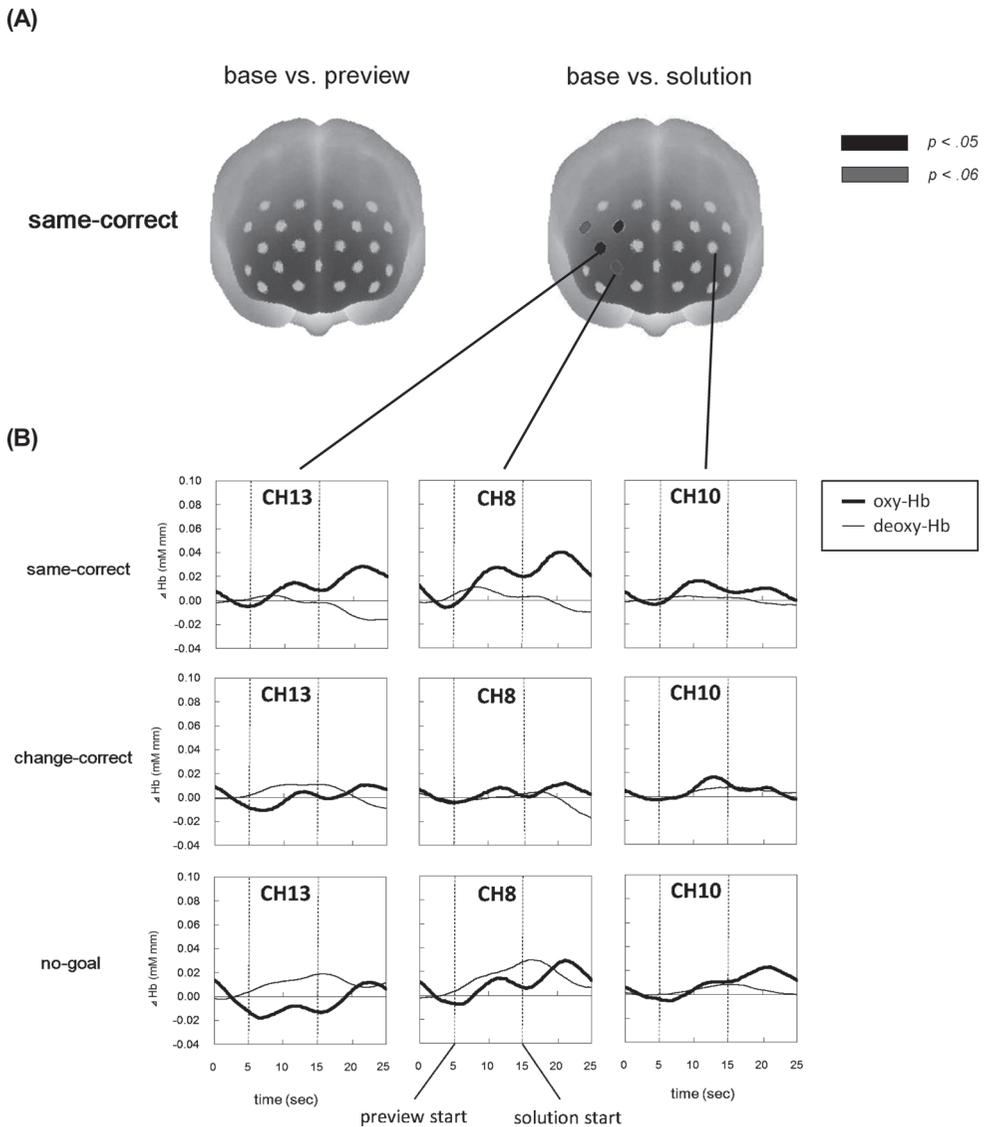


Figure 4. NIRS results. (A) Statistical p-maps of oxy-Hb increase during the first peak (preview phase) and the second peak (solution phase) in contrast with the baseline period, shown for the same-correct trials. Channels with significant/marginally significant oxy-Hb increase are marked with different colors (FDR corrected $p < .05$, and $p < .06$). The figure was drawn using POTATO. P-maps for the other response types are not shown because data from no channels revealed statistical significance. (B) Time course for signal changes of oxy- and deoxy-Hb in representative channels (CHs 8, 10, and 13), shown for each response type. The graphs represent the grand average of all participants. The dashed lines in each graph represent the moment the preview phase started and the moment the solution phase started following the preview, respectively.

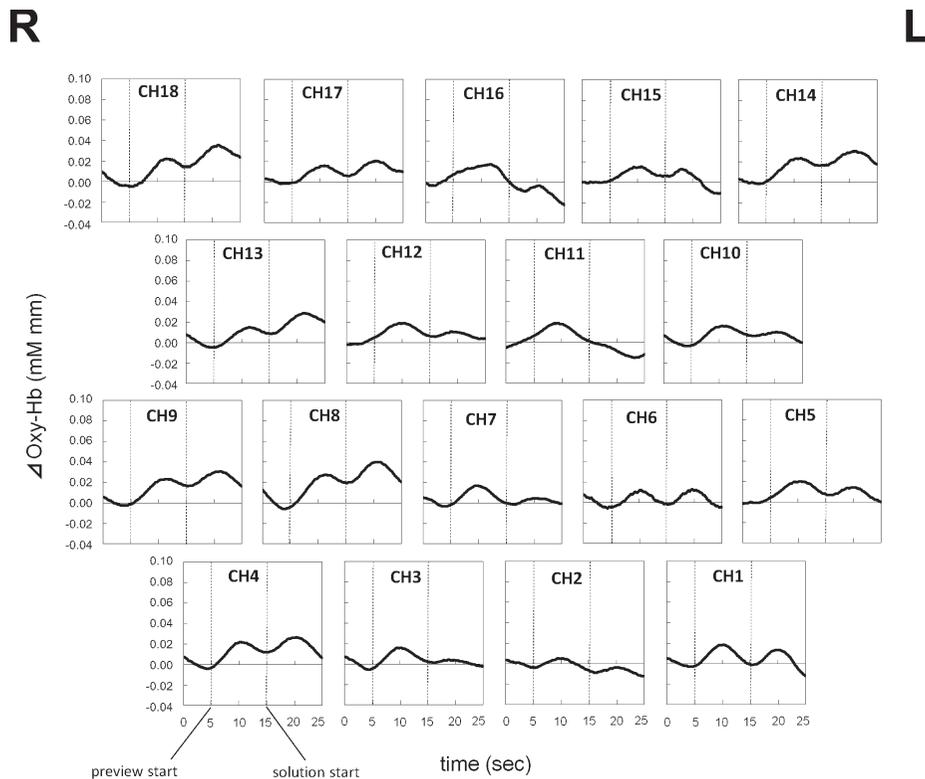


Figure 5. Time course for signal changes of oxy-Hb in the same-correct trials for all the analyzed channels (CHs 1–18), to show the hemodynamic change patterns having two peaks. The graphs represent the grand average of all participants. The dashed lines in each graph represent the moment the preview phase started and the moment the solution phase started following the preview, respectively.

cortex; CHs 13 and 18: middle frontal cortex, according to the virtual registration method by Tsuzuki et al. (2007). Thus, in these same-correct trials, oxy-Hb significantly increased 3–7 s after the start of the maze solution especially in right prefrontal areas. For the change-correct and no-goal trials, no significant hemodynamic changes were found in any channels either during the preview (change-correct: $t = -1.701 - 0.777$, $p_s > 0.100$; no-goal: $t = -2.158 - 1.169$, $p_s > 0.040$) or the solution phase (change-correct: $t = -3.189 - -0.274$, $p_s > 0.005$; no-goal: $t = -3.189 - -0.274$, $p_s > 0.005$). Figure 4(B) depicts the time course of Hb changes from several representative channels. Figure 5 also shows changes in oxy-Hb for the same-correct trials for all of the 18 analyzed channels. These waveforms in many of the analyzed channels and response types have the first peak during the preview phase and the second one during the solution phase, most evidently in the same-correct trials compared with the other response types. Hemodynamic changes during the first peak, however, failed to reveal statistical significance in any channels/response types.

To examine the hemispheric differences in hemodynamic changes for the four channels that showed significant or marginally significant increases in oxy-Hb during the solution phase for the same-correct

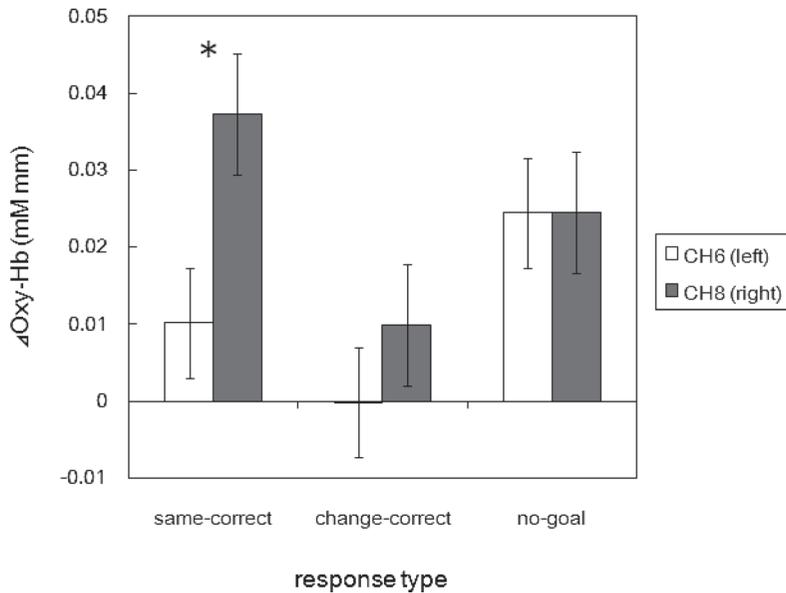


Figure 6. Oxy-Hb increase in CH8 and its counterpart in the left hemisphere, i.e., CH6, during the second peak (solution phase) in contrast with the baseline period, shown for each response type (i.e., same-correct, change-correct, no-goal). Error bars indicate standard errors of the mean. * $p < .05$.

trials, i.e., CHs 8, 13, 17, and 18, we directly compared these oxy-Hb changes with those in symmetrically located channels in the left hemisphere (CHs 6, 10, 15, and 14, 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 no-goal) as within-subject factors was conducted for each channel pair. Comparisons between CHs 10 and 13, CHs 15 and 17, and CHs 14 and 18, failed to reveal statistically significant outcomes. The comparison between CH8 (right) and CH6 (left) showed that the main effect of hemisphere ($F[1, 19]=4.600$, $p=0.045$) was significant, although the main effect of response type ($F[2, 38]=1.201$, $p=0.312$) or the interaction between these two factors ($F[2, 38]=1.707$, $p=0.195$) failed to reach statistical significance. Post-hoc comparisons by paired t -tests with Bonferroni correction revealed that increase in oxy-Hb for the same-correct trials was significantly larger in CH8 than in CH6 ($t[19]=-2.630$, $p=0.016$), although for the other response types direct comparisons between channels failed to show statistical significance (change-correct: $t[19]=-1.244$, $p=0.229$; no-goal: $t[19]=-0.002$, $p=0.998$) (Figure 5; see Figure 6 as well). These results show that at least CH8 showed significantly greater increase in oxy-Hb during the solution phase of the same-correct trials than the counterpart in the left hemisphere.

We further explored whether there are individuals showing significant hemodynamic changes during the preview phase. All the ten same-correct trials (*not* trials for the other response types) were considered for this analysis. For each participant, increase in oxy-Hb during the preview phase in contrast with the baseline period was evaluated using paired t -tests. One participant (a male, 24 years)

showed significant hemodynamic changes during the preview phase in five channels: CH1($t[9]=4.265$, $p=0.002$), CH2 ($t[9]=5.000$, $p=0.001$), CH3($t[9]=4.206$, $p=0.002$), CH17($t[9]=4.709$, $p=0.001$), and CH18($t[9]=4.832$, $p=0.001$). Another participant (a male, 24 years) revealed significant oxy-Hb increase in CH18 ($t[9]=4.994$, $p=0.001$), and also another one (a male, 24 years) in CH17($t[9]=7.534$, $p=0.000$). No significant hemodynamic changes during the preview phase were found for other participants or channels. Thus, for most participants and channels hemodynamic changes during the preview phase failed to reach statistical significance, except for just a few cases.

DISCUSSION

The present study using near-infrared spectroscopy examined prefrontal activation in adult humans performing an eight-arm *shuriken*-shaped maze task presented on a touch screen that was previously used for pigeons to assess preplanning processes. Adult humans in this study exhibited fewer incorrect responses compared to avian subjects in previous studies, even immediately after the goal jumped to another location following the preview phase (proportion of errors: 50.9% for pigeons; 1.7 % for adult humans). This suggests that human adults employ better inhibition and flexible changing of behavior when confronted with unexpected events during the course of a trial. Our previous study using a plus-shaped maze task showed that adult humans made fewer errors than pigeons or human children immediately after the goal location changed during the course of maze solution (Miyata et al., submitted). Both this preceding result and the present data on the behavioral level are in agreement with the notion that human adults are superior in abilities for inhibition and flexibility from both evolutionary as well as developmental perspectives. This appears consistent with human adults' developed executive function of the frontal cortex.

The NIRS data collected during and before the maze task suggests different patterns of hemodynamic changes in the prefrontal area according to each behavioral pattern. In the baseline, same-correct trials, activation associated with task performance, i.e., increase in oxy-Hb concentration after the start of maze solution, was observed in some channels located around the right superior-middle prefrontal cortices. This seems in agreement with the previous findings from neuroimaging studies suggesting that the right 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). On the other hand, in the change-correct and no-goal trials no significant hemodynamic changes associated with maze solution was observed in any channels. Change-correct trials seem to reflect cases in which preplanned actions were successfully inhibited faced with the goal-shift, followed by directing for a new goal without making errors. This inhibition and subsequent reengagement was probably not demanding for the participants, considering that they made very few errors toward the previous goal. No-goal trials did not allow chances to plan forward during the preview phase, in which participants could not use outcomes of preplanning for maze solution. Thus, these hemodynamic change patterns showing significant activation in the same-correct trials but not in the other response types suggests that neuronal activities associated with maze solution are largest when participants have the same

task as they preplanned during prior observation.

Hemodynamic changes during the preview phase failed to reach significance in any channels or response types, even though NIRS waveforms often showed one peak during this phase (Figures 4[B], 5). These overall insignificant trends are in good contrast with our previous study using a plus-shaped maze (Miyata et al., submitted), which revealed significant activation associated with planning and inhibition/reengagement in many channels of the prefrontal area. Whereas this previous study investigated neuronal activation *while* performing on the maze, the present study intended to explore planning *before* starting to solve the maze. It is possible that the participants preplanned the solution of the maze to a certain extent, but pure observation without acting on the task may not have facilitated them to preplan a lot. Planning as well as cognition like inhibition and subsequent reengagement faced with task changes may be done more extensively while subjects are actually engaged in cognitive activities, than while they are mentally rehearsing such activities without actions.

The present NIRS data suggest individual differences in prefrontal cortex activation associated with preplanning. Whereas most participants failed to show significant activation during the preview phase, at least three participants showed relatively large increase in oxy-Hb which reached significance in one or more channels. This may imply that there were some individuals who used more cognitive resources for preplanning the maze solution compared with the others. Differences among participants may exist in the motivation to solve the task, such that they would use more or smaller amount of cognition during the pure observation period.

A possible problem with the present task is that the maze used here was too simple to reveal preplanning in human adults. Actually, participants in this study made few errors, with first response latencies showing no statistically significant difference between any test conditions. NIRS data also failed to reveal significant activations during the preview phase, even though waveforms having one peak during this period were observed. This may be because the task did not place much cognitive load for the adults. To facilitate these participants to more elaborately plan the solution of problems during the preview phase, it would be promising to use more difficult maze (or other) tasks. Because with the present navigation paradigm it would be difficult to make the problems much more complex, a possible way forward could be to use difficult 2-D mazes, like the ones used for the computer games, which take adults ten or more seconds for solution.

To summarize, the present NIRS study showed that adult humans performed a computerized *shuriken*-shaped maze task having a preview phase with better behavioral flexibility compared to pigeons. In addition, hemodynamic change data provided implication for the time course of two neurocognitive processes associated with preplanning and task solution. Because NIRS can be used safely 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 navigation and planning at the neuronal level. Actually, if presented for young children, the present maze task may place sufficient cognitive load to reveal activation associated with preplanning. Also, by using similar maze tasks, it would be possible to explore the neuronal bases of spatial navigation and preplanning 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.

REFERENCES

- Antonova E, Parslow D, Brammer M, Dawson GR, Jackson SH, Morris RG (2009): Age-related neural activity during allocentric spatial memory. *Memory* 17: 125–143.
- Baker SC, Rogers RD, Owen AM, Frith CD, Dolan RJ, Frackowiak RS, Robbins TW (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, Druke B, Vorhold V, Knops A, Philippen B, Gauggel S (2010): When response inhibition is followed by response reengagement: An event-related fMRI study. *Hum Brain Mapp*. Published online. DOI: 10.1002/hbm.21001.
- Correia SPC, Dickinson A, Clayton NS (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 JP (1997): A hierarchical neuronal network model for planning behavior. *Proc Natl Acad Sci U S A* 94: 13293–13298.
- Eagle DM, Robbins TW (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 NJ, Clayton NS (2001): Effects of experience and social context on prospective caching strategies in scrub jays. *Nature* 414: 443–446.
- Folley BS, Astur R, Jagannathan K, Calhoun VD, Pearlson GD (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 TA (2004): Inhibition of ongoing responses in patients with Parkinson's disease. *J Neurol Neurosurg Psychiatry* 75: 539–544.
- Ghatan PH, Hsieh JC, Wirsén-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 JJ (2009): Age differences in the formation and use of cognitive maps. *Behav Brain Res* 196: 187–191.
- Iversen IH, Matsuzawa T (2003): Development of interception of moving targets by chimpanzees (*Pan troglodytes*) 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*) on “traveling salesperson” navigation tasks presented on an LCD screen. *J Comp Psychol Advance online publication*. doi:10.1037/a0019931.
- Miyata H, Gajdon GK, Huber L, Fujita K (2010): How do keas (*Nestor notabilis*) solve artificial-fruit problems with

- multiple locks? Anim Cogn Published online. DOI: 10.1007/s10071-010-0342-9.
- 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, 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, Watanabe S, Minagawa-Kawai Y submitted: Two neurocognitive processes in the prefrontal cortex during a computerized maze task: A near-infrared spectroscopy study. *Brain Res*
- Moffat SD (2009): Aging and navigation: what do we know and where do we go? *Neuropsychol Rev* 19: 478–489.
- Moffat SD, Elkins W, Resnick SM (2006): Age differences in the neural systems supporting human allocentric spatial navigation. *Neurobiol Aging* 22: 787–965–972.
- Mulcahy NJ, Call J (2006): Apes save tools for future use. *Science* 312: 1038–1040.
- Mushiaki 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 RC (1971): The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 9: 97–113.
- Owen AM (1997): Cognitive planning in humans: neuropsychological, neuroanatomical and neuropharmacological perspectives. *Prog Neurobiol* 53: 431–450.
- Pantelis C, Barnes TR, Nelson HE, Tanner S, Weatherley L, Owen AM, Robbins TW (1997): Frontal-striatal cognitive deficits in patients with chronic schizophrenia. *Brain* 120: 1823–1843.
- Raby CR, Alexis DM, Dickinson A, Clayton NS (2007): Planning for the future by western scrub-jays. *Nature* 445: 919–921.
- Robbins TW (1998): Dissociating executive functions of the prefrontal cortex. In: Roberts TW, Weiskrantz L, editors. *The Prefrontal Cortex. Executive and Cognitive Functions*. Oxford Univ. Press, Oxford, pp 117–142.
- Rubia K, Russell T, Overmeyer S, Brammer MJ, Bullmore ET, Sharma T, Simmons A, Williams SC, Giampietro V, Andrew CM, 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, Mushiaki H, Tanji J (2007): Categorization of behavioural sequences in the prefrontal cortex. *Nature* 445: 315–318.
- Singh AK, Dan I (2006): Exploring the false discovery rate in multichannel NIRS. *Neuroimage* 33: 542–549.
- Suddendorf T, Corballis MC (1997): Mental time travel and the evolution of the human mind. *Genet Soc Gen Psychol Monogr* 123: 133–167.
- Tsuzuki D, Jurcak V, Singh AK, Okamoto M, Watanabe E, Dan I. (2007): Virtual spatial registration of stand-alone fNIRS data to MNI space. *Neuroimage* 34: 1506–18.
- Tulving E (1983): *Elements of episodic memory*. Oxford, England: Clarendon Press.
- 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.
- van den Heuvel OA, Groenewegen HJ, Barkhof F, Lazeron RHC, van Dyck R, Veltman DJ (2003): Frontostriatal system in planning complexity: a parametric functional magnetic resonance version of Tower of London task. *NeuroImage* 18: 367–374.
- Veale DM, Sahakian BJ, Owen AM, Marks IM (1996): Specific cognitive deficits in tests sensitive to frontal lobe dysfunction in obsessive-compulsive disorder. *Psychol Med* 26: 1261–1269.