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Medial prefrontal cortex–dorsal anterior cingulate cortex connectivity during behavior selection without an objective correct answer

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ABSTRACT

Life choices (e.g., occupational choice) often include situations with two or more possible correct answers, thereby putting us in a situation of conflict. Recent reports have described that the evaluation of conflict might be crucially mediated by neural activity in the dorsal anterior cingulate cortex (dACC), although the reduction of conflict might rather be associated with neural activity in the medial prefrontal cortex (MPFC). What remains unclear is whether these regions mutually interact, thereby raising the question of their functional connectivity during conflict situations. Using psychophysiological interaction (PPI) analyses of functional magnetic resonance imaging (fMRI) data, this study shows that the dACC co-varied significantly higher with the MPFC during an occupational choice task with two possible correct answers when compared to the control task: a word-length task with one possible correct answer. These results suggest that the MPFC has a functional relation with dACC, especially in conflict situations where there is no objective correct answer. Taken together, this lends support to the assumption that the MPFC might be crucial in biasing the decision, thereby reducing conflict.

Life choices often include situations with two or more possible correct answers. For example, when we choose our own occupation, plural possible correct answers might exist (teacher, lawyer, doctor, etc.); we cannot know whether the selected occupation is objectively correct. How does the brain respond to such conflict-ridden situations?

Conflict arises when incompatible response tendencies are active simultaneously [1]. The abilities of monitoring and regulation of conflict have been investigated extensively in neuroscience. Their focus has been predominantly on behavior selection with two (or more) choices with only one correct answer entailing the possibility of error as for instance during the Stroop task [27]. A number of neuroimaging studies have documented that greater dorsal anterior cingulate cortex (dACC) activation is observed when participants are confronted with situations requiring detection of conflict [5,9,12,13], while the cognitive regulation of conflict (e.g., attentional modulation) is apparently related to the lateral prefrontal cortex (LPFC) to reduce conflict [1,9].

There are, however, situations in which we are confronted with many possible correct answers with none being a readily apparent erroneous answer. The absence of an objectively correct answer seems to go along with the additional recruitment of the medial prefrontal cortex (MPFC; Brodmann area 9, 10) accompanying activation in dACC. For instance, Moll et al. [14] investigated charitable donation behavior that occurred as participants anonymously donated to or opposed donation to real charitable organizations related to major societal causes. Results showed that costly decisions (choosing costly donation or opposing costly donation) were associated with activation of the MPFC and dACC compared with pure reward decision. Similarly, the dACC and the MPFC activations during behavior selection with two possible correct answers were reported from Greene et al. [8] using a cheating task.

The dACC is thought to mediate the evaluation of conflict between possible correct answers, although the MPFC is thought to associate with reduction of the conflict by biasing either choice of behavior [2,11,16–20,25,28]. Nakao et al. [16,17] proposed that representations in the MPFC, for example, representation of one's own personal traits (self-knowledge) [21], representation of a familiar person's personal traits [26], one's own mental state [10], another person's mental state (theory of mind) [22], morality [15], knowledge related to social scripts [29], and representation of rewards [3] have a function of reducing conflict among many possible correct

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answers by biasing either choice of behavior. Nakao et al. hypothesized that, for example, an occupation is chosen based on MPFC representations such as personal aptitudes (self-knowledge), a parent's demands (representation of a familiar person's knowledge and theory of mind), and salary (rewards). To examine this hypothesis, Nakao et al. [19] used an occupational choice task (e.g., which occupation do you think you could do better?—dancer or chemist) with two possible answers and manipulated the degree of conflict. They observed that the dACC was activated when the conflict during occupational choice was large, and that the MPFC was activated more in the occupational choice task than in the word-length task (e.g., which word is longer?—dentist or comedian), which has a correct answer. Furthermore, Nakao et al. [18,20] showed that self-knowledge reference – which activates MPFC [21,26] – biases behavior selection in occupational choice and decreases conflict during occupational choice using event-related brain potentials (ERPs).

What remains unclear is whether these regions truly mutually interact. More specifically, it remains unclear whether the dACC is connected to the MPFC during situations with two possible objectively correct answers when compared to those situations with only one correct answer. This is particularly relevant because the MPFC is recruited only during the former situations, as described above, but not during the latter. The aim of the present study is to examine whether the MPFC has functional connectivity (i.e., temporal correlations of activity across spatially distributed brain regions) with dACC only in a situation with more than one possible correct answer. We also examine the connectivity between the dACC and other regions (posterior cingulate cortex; PCC and medial temporal lobe; MTL) observed in Nakao et al. [19] that might also have a function of conflict reduction [11,19]. We therefore conducted psychophysiological interaction (PPI) analyses [6], using previously published functional magnetic resonance imaging (fMRI) data [19], to identify regions that are functionally connected to the seed region more strongly in one psychological context or variable than in another. We hypothesized here that the MPFC has increased functional connectivity with dACC in a situation with more than one possible correct answer, i.e., the occupational choice task, than in a situation with a single correct answer.

From Nagoya University, 14 healthy participants (7 male, mean age 22.1 years, range 19–27) were recruited. All participants were right-handed and had normal vision. They were free of neurological or psychiatric disorders. The present study was approved by the Ethics Committee of Kizawa Memorial Hospital. In accordance with the Declaration of Helsinki, written informed consent was obtained from each participant before the investigation.

Details of the study protocol and the task procedure were described in Nakao et al. [19]. In brief, the stimuli were 216 occupation-related words. Participants performed tasks of two types: an occupational choice task and a word-length task. In these tasks, two occupational words were presented on the right and left sides of the screen. Participants selected either of the two by pressing the button on the corresponding side. For the occupational choice task, participants selected an occupation that they believed they could perform better than the other ("Which occupation do you think to do better?"). For the word-length task, participants selected a longer occupation word ("Which word is longer?"). Each task used two conflict conditions: large-conflict conditions and small-conflict conditions. In these tasks, the conflict was manipulated based on the difference of the word sets. In the occupational choice task, 27 word pairs were designated for each conflict condition based on values of ratings (1–4) for how well participants thought they could perform in the occupation: word pairs with equal differences in their respective rating values were assigned to a Large-conflict condition, and word pairs for which the difference of the rating value was two or three were assigned to Small-conflict condition (see Supplementary Fig. 1(a)). The ratings were assigned by each participant 7–10 days before the fMRI experiment. In the word-length task, 27 word pairs were designated for each conflict condition based on differences of word-length: word pairs for which the difference of the word-lengths was one were assigned to the Large-conflict condition, and word pairs for which the difference of word-lengths was more than two were assigned to the Small-conflict condition. With these restrictions, the words were assigned randomly to these conditions.

As the fMRI experiment, participants performed 12 blocks of 9 trials of tasks (3 blocks per each condition). The order of blocks was randomized across participants with the restriction that the same conditions were not presented contiguously. The order of trials within each condition and the presentation side of words were randomized across participants. On the display, a question sentence, stimulus words, and a rectangle surrounding these stimulus words were presented: the stimulus words and the rectangle were presented beneath the question sentence (see Supplementary Fig. 1(b)). Each block began with the appearance of the question sentence and the rectangle. Then, 3400 ms later, two stimulus words appeared right and left within the rectangle. The stimulus word remained onscreen for 600 ms. After a 3400 ms pause, the next trial began (i.e., the next stimulus words were presented). Participants responded to each stimulus using index fingers on left and right response buttons until the next trial began. At the end of each block, the question sentence was removed with a stimulus word; after 17,600 ms, the next block began.

After the experiment, for the Small-conflict condition of Occupational choice, the mismatch rate was calculated for each participant. The mismatch rate indicates the rate of trials of mismatch between the rating value of each occupation and the judgment of the Occupational choice task: for example, for a case in which the participant rated Banker as 4 and Angler as 1, and chose Angler in the occupational choice task, we counted the trial as a mismatch.

Image acquisition, spatial analysis and conventional analysis were described in Supplementary Methods and Nakao et al. [19]. The PPI analyses of connectivity were performed in the seed point of the maximum activation areas within the MPFC ($x, y, z = -4, 56, 16$) and PCC ($x, y, z = -6, -52, 4$) identified in the conventional second level analysis of the task comparison (occupational choice > word-length). Although the activated area of MPFC was extended to the rostral ACC, local maxima within the MPFC (Brodmann area 10) were used based on the results of previous studies [7,16,17,25], which showed that not the rostral ACC but the MPFC has a dominant role in biasing behavior selection. Additionally, the maxima identified in the conventional second level analysis of the Large-conflict > Small-conflict contrast of occupational choice task (left MTL: $x, y, z = -44, 6, -18$, and right MTL: $x, y, z = 46, -4, -18$, dACC: $x, y, z = -10, 24, 30$) were also seeded for PPI analyses. In the first level analysis, for each participant, the time series of the 3-mm radius sphere of each coordinate of seed regions were extracted to generate the time series of the neuronal signal as the physiological variable in the PPI. The psychological variables represented the contrasts of tasks (occupational choice > word-length) or degree of conflict in occupational choice task: The bilateral MTL and dACC seed PPIs were conducted not only for the contrasts of tasks, but also for the degree of conflict in the occupational choice task because the activation of these regions was found in the conventional analysis of the Large-conflict > Small-conflict contrast of occupational choice task. An additional regressor represented the interaction between the psychological and physiological factors. These regressors were convolved with the canonical hemo-dynamic response function and entered into the regression model. The effect of the interaction term was examined using the contrast [100], in which the first column represents the interaction term. At the second level, the resulting images of contrast estimates from each participant were

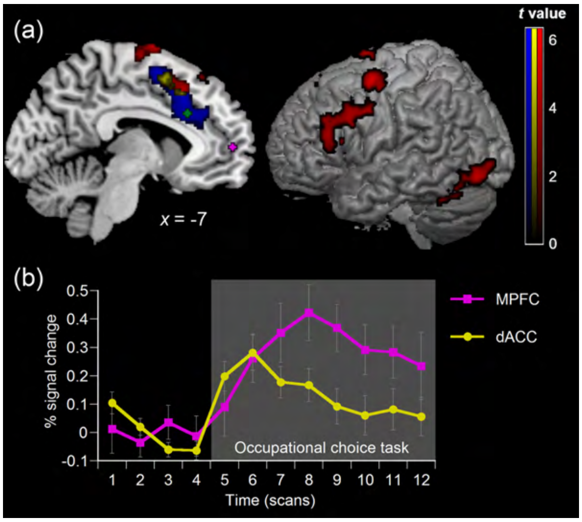

Fig. 1. (a) Regions showing increased connectivity with the medial prefrontal cortex (MPFC) during occupational choice (results of psychophysiological interaction (PPI) analysis) and regions showing increased activity in Large-conflict > Small-conflict contrast of occupational choice (results of conventional analysis reported in Nakao et al. [19]). Voxels observed in both analyses are shown in yellow. The brightness scale of yellow denotes the *t*-value in the PPI analysis. Red voxels were observed in the PPI analyses, but not in the conventional analyses. Blue voxels were observed in the conventional analyses, but not in the PPI analyses. Purple voxels show the seed region within MPFC. Green voxels show the seed region within dACC, the coordinate of which was selected from Large-conflict > Small-conflict contrast of occupational choice. This figure was constructed using software (MRIcron; http://www.sph.sc.edu/comd/rorden/MRicron/). (b) Percent signal change graphs depicting group-averaged responses to the occupational choice task obtained from the seed MPFC region and significantly observed areas within the dorsal anterior cingulate cortex (dACC) in PPI analyses. Error bars represent the standard error of the mean signal change at each scan number. The first four scans are the scans conducted during rest. (For interpretation of the references to color in text, the reader is referred to the web version of the article.)

used for the random effect group analysis. Statistical images were acquired using the same threshold used in the conventional analysis by Nakao et al. [19] (an uncorrected voxel threshold of $p < 0.005$ and corrected cluster threshold of $p < 0.05$). For PPI analysis, we used a tool implemented in SPM5. In addition, for each participant, software (MarsBar; http://marsbar.sourceforge.net/) was used to extract time-course fMRI data. Four scans before each block were used as the baseline to calculate the percent signal change. To examine the correlation between the magnitude of the brain area coupling and behavioral measures, mean beta values from significantly observed areas in PPI analysis were extracted using the Marsbar software.

Behavioral results and results of conventional analyses were described previously by Nakao et al. [19]. The PPI analysis results (Table 1 and Fig. 1(a)) demonstrated that activity in the MPFC was accompanied by task-dependent (occupational choice > word-length) functional interaction with specific areas: dACC extending to the paracingulate cortex, LPFC, pre-motor cortex, and inferior occipital gyrus. In other words, the covariance in activity between the seed region (MPFC) and these regions during occupational choice was significantly higher than that during word-length judgment. The dACC region found in the PPI analysis shared a similar region to that observed in the conventional analysis of the Large-conflict > Small-conflict contrast of occupational choice task, which had been reported already in Nakao et al. [19] (see Fig. 1(a)). To confirm the functional connectivity between dACC and MPFC, we also conducted PPI analysis using a seed of dACC (x, y, $z = -10$, 8, 54), which was observed in MPFC seed PPI, in occupational choice > word-length contrast. The MPFC (BA 10, coordinates of maximum = −2, 54, 14, cluster size = 56, $t = 4.92$) was observed using an uncorrected voxel threshold of $p < 0.001$ and corrected cluster threshold of $p < 0.05$. The PPI analyses using PCC, bilateral MTL, and dACC seeds in the context of occupational choice > word-length contrast did not reveal a significant effect. No pattern of coupling was observed in the bilateral MTL and dACC seeds PPI analyses in Large-conflict > Small-conflict contrast of occupational choice task.

Fig. 1(b) presents the mean percent signal changes during the occupational choice task obtained from the seed MPFC region and the dACC region found in the PPI analysis. A pattern was apparent that the dACC activation increased in advance of the MPFC activations during the occupational choice task, and the dACC activation started to decrease when the MPFC activation was increased.

For each participant, the PPI beta value (a measure of task-dependent functional connectivity) of the significantly observed area in MPFC seed PPI analysis was extracted to conduct correlation analysis between participants with behavioral measurements. To avoid effects of outliers, Spearman's rank-correlation coefficients were calculated. The correlation analysis revealed significant negative correlation between the extent of MPFC-dACC coupling and the mismatch rate ($rs = -0.55$, $p < 0.05$).

This study was undertaken to examine whether each of the MPFC and other regions (the PCC and the MTL) have functional connectivity with dACC during conflict situations without an objective correct answer. The results of conventional analysis reported in Nakao et al. [19] are in accordance with those of previous studies: similar to previous studies, we demonstrated the additional recruitment of the MPFC during situations in which there is more than one correct answer [8,14]. Our results reported herein extend these previous findings, showing functional connectivity between the MPFC and the dACC: MPFC seed PPI showed significant covariance in activity with the dACC during the occupational choice task although no co-variation existed during the word-length task. The region of dACC found in PPI was similar with the region found in conventional analysis of Large-conflict > Small-conflict of occupational choice task. These suggest that the functional connectivity between dACC and MPFC might be crucial in mediating the conflict that is present in situations without one correct answer. This is even more remarkable when considering that the other regions recruited during our occupational task choice, the PCC and the MTL, showed no significant covariance with the dACC either.

Although the MPFC seed PPI showed significant covariance in activity with the dACC, the PPI analysis using the dACC seed – the coordinate of which was selected from Large-conflict > Small-conflict contrast of occupational choice – revealed no covariance with MPFC (even when using an uncorrected voxel threshold of $p < 0.001$ and a corrected cluster threshold of $p < 0.05$). This discrepancy can be attributed to the difference of sub-regions of dACC. As Fig. 1(a) shows, the seed region of dACC (represented as green voxels) was an inferior region of dACC relative to the region observed in the MPFC seed PPI. Actually, MPFC was observed in the PPI analysis using a dACC seed, the coordinate of which was selected from the result of MPFC seed PPI. These results suggest that not the inferior region but the superior region of dACC has a functional relation with MPFC.

Our results suggest a special importance of the functional connectivity between dACC and MPFC in conflict situations. What remains unclear is the exact mode of how the two regions mutually interact. One possible explanation would be that the dACC modulates the MPFC activity. This causal relation is thought to correspond to the process described in Nakao et al. [16,17]: when the conflict is detected in dACC, the behavioral criteria represented in MPFC is activated: as the regulation process to reduce conflict, the MPFC is activated in reaction to dACC activation, especially when no objective correct answer exists. Although the time resolution of fMRI is low and we used a block design, consistent with this explanation,

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Table 1
Locations found through PPI analysis.

Comparison, seed region, and brain region of co-activation	Brodmann areas	Side	Coordinates			Cluster size	*t*-Value
			x	*y*	*z*		
Occupation > word-length							
Seed: medial prefrontal cortex (−4, 56, 16)							
Dorsal anterior cingulate cortex/paracingulate cortex	6/32	Left	−10	8	54	671	5.21
Lateral prefrontal cortex	8/9	Left	−28	14	38	1212	5.20
Pre-motor cortex	6	Left	−22	−8	52	638	6.37
Inferior occipital gyrus	19/37	Left	−42	−76	−10	468	5.20
Seed: dorsal anterior cingulate (−10, 24, 30)	No significant cluster						
Seed: posterior cingulate cortex (−6, −52, 4)	No significant cluster						
Seed: left middle temporal lobe (−44, 6, −18)	No significant cluster						
Seed: right middle temporal lobe (46, −4, −18)	No significant cluster						
Occupation (Large-conflict > Small-conflict)							
Seed: dorsal anterior cingulate (−10, 24, 30)	No significant cluster						
Seed: left middle temporal lobe (−44, 6, −18)	No significant cluster						
Seed: right middle temporal lobe (46, −4, −18)	No significant cluster						

the pattern presented in Fig. 1(b) shows that the dACC activation increased in advance of the MPFC activations during the occupational choice task. This regulatory process is structurally similar to the regulation process in the situation where an objective correct answer exists: the lateral prefrontal cortex activation is increased after the conflict is detected in dACC [6].

An alternative explanation is that the MPFC activity causes dACC activity. Nakao et al. [16–18,20] described that the MPFC reduces conflict detected in dACC by biasing either choice of behavior. Therefore, one might infer that the more MPFC is activated, the less dACC is activated during the entire time of the behavior selection. Thereby, results reported by Nakao et al. contradict the result of PPI in which the activation of dACC co-varies with MPFC. Theoretically, however, the biasing function of the MPFC does not mean that, during of the entire behavior selection time, the more MPFC is activated the less dACC is activated. The MPFC is thought to represent criteria of various kinds to choose one's own behavior [16–18,20], possibly including representation of one's own and [21] a familiar person's personal traits [26], one's own [10] another person's mental state [22], morality [15], knowledge related to social scripts [29], and representation of rewards [3]. From these representations of many kinds, the representations which bias behavior ultimately are thought to be determined by competition through the inhibitory connection among biasing representations, as in the model proposed by Rolls et al. [4,25]. At the beginning of the processing, no biasing representation is activated much more than the others; they are in competition (see Deco and Rolls [4]; fig. 6(a)). The conflict, which is calculated as the Hopfield energy [1], increases until the activation of some biasing representations increases sufficiently to inhibit the other biasing representations and to bias one choice of output. In agreement with this explanation, the pattern in Fig. 1(b) shows that the activations of both dACC and MPFC increase at the beginning of the occupational choice task and dACC activation started to decrease when the MPFC was activated strongly. Although we cannot specify the psychological process entailed by each causal relation between MPFC and dACC from this study, it is likely that both causal relations exist because a reciprocal anatomical connection between the MPFC and dACC is supported by results of studies of other primates [23,24].

The result of between participant correlation analysis is consistent with the explanation that the behavioral criteria represented in MPFC reduces conflict detected in dACC by biasing either choice of behavior [16–18,20]. A significant negative correlation was found between the extent of MPFC-dACC coupling and the mismatch rate. This result indicates that, for participants who showed stronger MPFC-dACC coupling in the occupational choice task than the word-length task, the judgments in the occupational choice task were more consistent with the ratings that had been conducted 7–10 days before the fMRI experiment. It is thought that participants who had strong functional connectivity between MPFC and dACC showed consistent judgment because behavioral criteria in MPFC function reduce conflict effectively in situations with more than one possible correct answer.

In conclusion, our study has provided new findings related to the functional relation among brain regions that function during behavior selection. Results showed that the MPFC has a dominant functional relation with dACC, especially in conflict situations for which no objective correct answer exists. These results lend support to the notion that MPFC has a role biasing behavior selection, thereby reducing conflict [16–20,25]. The functional connectivity between MPFC and dACC is expected to have an important role in behavior selection when people cannot detect an objectively correct answer.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neulet.2010.07.041.

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