Human Movement Science 63 (2019) 45–52

Contents lists available at ScienceDirect

Human Movement Science

journal homepage: www.elsevier.com/locate/humov

Cerebellar contributions to tactile perception in people with varying sensorimotor experiences: Examining the sensory acquisition hypothesis

Yu-Chien Lo[b], Chun-Ming Chen[b], Wu-Chung Shen[b,c], Yu-Ling Shih[a,*]

[a] *Department of Sport Performance, National Taiwan University of Sport, No. 16, Section 1, Shuang-Shih Road, Taichung 404, Taiwan, ROC*
[b] *Department of Radiology, China Medical University Hospital, 2 Yude Road, Taichung 404, Taiwan, ROC*
[c] *Department of Biomedical Imaging and Radiological Science, College of Health Care, China Medical University, No. 91, Hsueh-Shih Road, Taichung 404, Taiwan, ROC*

ARTICLE INFO

Keywords:
Cerebellum
Sensory acquisition
Tactile discrimination
Sports

ABSTRACT

The sensory acquisition hypothesis states that the sensory demand of a task is the most crucial factor in determining the level of cerebellar activity. The present study was conducted to examine whether the prediction of sensory demand holds when participants have different sensorimotor training experiences. Archery athletes and non-athletic control participants were asked to perform tactile discrimination tasks during fMRI scanning. In archery athletes, a pattern of reduced cerebellar activation accompanying higher sensory cortical activity was observed, whereas in non-athletic control participants the visual network was found to be in concert with extensive cerebellar activation. These findings are in accordance with the prediction that the cerebellum plays a supportive role for the cerebral cortex in sensory data acquisition.

1. Introduction

Over the past two decades, research on the cerebellum has been shifting from motor control and learning to higher cognitive functions, such as memory and language. Supported by evolutionary (Weaver, 2005), anatomical (Dum & Strick, 2003) and neuroimaging evidence (Stoodley & Schmahmann, 2008), it is now widely accepted that the cerebellum participates in various functions, both in motor and non-motor domains, through its densely reciprocal connections with the cerebral cortex. The uniformity of the cerebellar cytoarchitecture has led to the hypothesis that computations performed by the cerebellum are the same for numerous functions associated with the cerebellum. Different functions of the cerebellum are fulfilled depending on its cortical afferents (Ito, 2008).

Many theories about computation by the cerebellum have been proposed to explain its contributions to various functions (Blakemore, Wolpert, & Frith, 1998; Bower, 1997; Imamizu et al., 2000; Ivry & Keele, 1989; Wolpert & Ghahramani, 2000). The sensory acquisition hypothesis is one of the most prominent hypotheses among these theories (Bower, 1997). According to this hypothesis, the cerebellum serves as a meta-systemic sensory coordinator for monitoring and adjusting the acquisition of sensory information on which other brain regions are dependent. It supports the processing capabilities of the dependent brain regions, especially when careful control of incoming sensory data is required. To this end, cerebellar activity should be directly correlated with the computational demand of sensory information. As a support structure, the cerebellum does not directly contribute to a

---

[*] Corresponding author.
E-mail address: ylshih2010@ntupes.edu.tw (Y.-L. Shih).

https://doi.org/10.1016/j.humov.2018.11.012
Received 24 September 2015; Received in revised form 23 November 2018; Accepted 26 November 2018

particular neuropsychological function. Instead, it facilitates the processing efficiency of other brain regions (Bower, 1997). The contributions of the cerebellum to the coordination of incoming sensory information has been studied using numerous motor, perceptual, and cognitive tasks, for example, tactile discrimination (Pastor, Day, Macaluso, Friston, & Frackowiak, 2004), auditory processing (Petacchi, Laird, Fox, & Bower, 2005), spatial orientation and judgment (Lee et al., 2005), visuospatial functions (Molinari & Leggio, 2007), semantic discrimination (Xiang et al., 2003), and duration discrimination (Rao, Mayer, & Harrington, 2001).

In accordance with the sensory acquisition hypothesis, it has been shown that task-related cortical areas strengthen their functional connections with the cerebellum instead of increasing their activation. In addition, relatively restricted cortical regions accompanying more extensive intra-cerebellar connections are engaged when integration of two kinds of sensory information supports the discrimination process. It is argued that cortical computation can be reduced by retrieving sensory information from the cerebellum in a well controlled manner (Shih et al., 2009; Shih, Yeh, Kuo, Tzeng, & Hsieh, 2010). In addition to supporting the efficiency of cortical processing, another prediction of the sensory acquisition hypothesis is that cerebellar activity is directly correlated with the sensory demand of the task. In an imaging study of the cerebellar dentate nucleus, stronger dentate activation was found in two tasks requiring tactile discrimination rather than tasks with rapid, coordinated, fine finger movements without tactile discrimination (Gao et al., 1996). As far as the sensory demand of the task is concerned, it could be manipulated not only by varying sensory difficulty, but also by different sensory training experience. For instance, the sensorimotor adaptation inherent in sports training may modulate the way the brain processes sensory information. In this regard, it is argued that one of the crucial characteristics differentiating elite athletes from novices is the ability to filter out irrelevant sensory information (Milton, Solodkin, Hlustik, & Small, 2007). Furthermore, it has been shown that tactile perception is more stable in archery athletes than non-experienced subjects (Kotani, Ito, Miura, & Horii, 2007). Hence, it is hypothesized that archery athletes require less participation of the cerebellum than non-athletic participants when performing the same tactile discrimination tasks.

2. Materials and methods

2.1. Participants

Two groups of participants, archery athletes and non-athletes, were recruited. Sixteen archery athletes (eight female, eight male; mean age ± $SD = 20 \pm 1.5$ years) were recruited from a professional sport university, and all were qualified at the professional level at the National Intercollegiate Athletic Games in Taiwan. All athletes had received specific sports training for more than four years and had regular archery training for at least two hours a day, five days a week. The 16 non-athletic participants (eight female, eight male; mean age ± $SD = 19 \pm 1.4$ years) were recruited from general universities and had never received any specific sports training. All participants were without any history of neuropsychiatric disorders. Each participant gave written consent prior to the experiment and a local ethics committee approved this study.

2.2. Tasks

A 2 × 2 factorial design (sensory demand × group) was implemented in the present study. Participants were instructed to grasp-and-drop LEGO blocks in the low tactile demand condition (LD) and to sense the number of dots on the LEGO blocks using their first three fingers in the high tactile demand conditions (HD) during fMRI (functional Magnetic Resonance Imaging) scanning. The size of the blocks varied with the number of dots. There were 4 types, i.e. 2, 4, 6 and 8, of dot number on the blocks, and were three of each in one bag. Participants placed their hands in the bag which was attached on their wrists (Please see Fig. 1). In the LD condition, participants were instructed to grasp a block with their left and right hand sequentially, and then drop the blocks in both hands simultaneously. For the HD condition, participants grasped a block with their left hand, and then found another block with the same

Fig. 1. The tactile discrimination task.

number of dots with their right hand. However, this instruction did not rule out the possibility that some participants might have performed the tactile discrimination task by matching the size of the blocks instead of the number of dots. During the tasks, participants couldn't see their hands and the blocks, but the instructions of the tasks were projected via a projector onto a screen at the subjects' feet. First, a colored hand was presented for 2000 ms (a red hand symbolized LD, while a green hand symbolized HD). Followed by a 400 ms "Go" command, another hand with only a white outline signaled the start of the movements. Participants were given 4800 ms to complete the trial. These two conditions were presented in different trial blocks. There were 5 trials in each block and 12 blocks were presented in random order for each condition. In between each block of trials, a 24-second resting period, with a fixation cross on the screen, was presented. It took about 100 min for each participant to complete the experiment.

2.3. MR image acquisition

Brain images were acquired on a 3T Siemens MRI system (Siemens, USA). The participants' heads were immobilized with a vacuum-beam pad in the scanner. The experiment was conducted in a block design as described above. A $T2^*$-weighted gradient EPI sequence was used for functional data (slice thickness = 4 mm, without inter-slice gap, TR = 2400 ms, matrix size = 64 × 64, FOV = 230 × 230 mm). Thirty-five slices were acquired for whole brain coverage. An additional five dummy scans were added at the beginning of each session to allow the MR signal to reach equilibrium, and were not included in the analysis. Anatomical images were collected using a high resolution T1-weighted, 3D gradient-echo pulse sequence (slice thickness = 1 mm, voxel size = 1 × 1 × 1 mm, matrix size = 224 × 224 mm, FOV = 224 × 224 mm, 160–180 slices).

2.4. Data analysis

Pre-processing and statistical analysis of MR images was performed by SPM8 (Statistical Parametric Mapping, Wellcome Trust Centre for Neuroimaging, London, UK). The functional scans were slice timing corrected, realigned, and unwrapped to correct for head movements before co-registering with the anatomical image. The functional images were then fitted to the Montreal Neurological Institute (MNI) proportional stereotaxic space and were spatially smoothed with an isotropic 8 mm FWHM Gaussian kernel. The pre-processed fMRI data were entered next into a first-level individual analysis to contrast fMRI activity during the task condition with the rest condition. The time series of each voxel was fitted with a corresponding task regressor that modeled a boxcar convolved with a canonical hemodynamic response function (HRF) with its temporal derivative.

In a second-level analysis, contrast images from the analysis of individual subjects were analyzed using a model of full factorial design, thereby generating a random-effects model and allowing for inference to the general population. The ANOVA model consisted of two factors, namely group (2 levels) and tactile demand (2 levels), and subsequent T tests were used to examine the group (between-subject) and the tactile demand (within-subject) effect. The statistic threshold was set to uncorrected $p < 0.001$, with a spatial extent threshold of 5 voxels. The anatomical location of cerebellum was labeled according to the MRI atlas of the human cerebellum (Schmahmann et al., 1999), and the result was visualized using xjView toolbox (http://www.alivelearn.net/xjview).

3. Results

The results of the main effect of the two factors, group and tactile demand, are listed in Tables 1 and 2. No significant effect of interaction was found between these two factors. The main effect of group revealed cortical activations in various somatosensory and visual areas, including the primary somatosensory (Brodmann area (BA) 2), somatosensory association (BA7), primary visual and secondary visual cortices (BA17, 18). Significant activation in the lobule V of cerebellum was also found for the main effect of group. For the main effect of tactile demand, in addition to the somatosensory association and the secondary visual cortices, the superior/middle frontal gyrus (BA8), precuneus (BA31), middle temporal gyrus (BA39) and fusiform gyrus (BA20, 37) activated differently between the HD and LD conditions. Furthermore, significant activations were found in the hippocampus, the lobule VI of cerebellum

Table 1
Brain activation foci showing significant differences ($p < 0.001$) between groups.

Cortical Region	Hemisphere	Brodmann Area	MNI Coordinates	Cluster-level Extent	F value ($F_{1,60}$)
Frontal Lobe					
Medial Frontal Gyrus	Left	6	−12, 0, 66	31	14.53
Parietal Lobe					
Precuneus	Left	7	−20, −82, 46	148	20.33
Postcentral Gyrus	Right	2	50, −32, 36	66	16.67
Inferior Parietal Lobule	Right	40	40, −50, 52	8	12.92
Occipital Lobe					
Lingual Gyrus	Right	17	14, −96, −8	132	19.54
Middle Occipital Gyrus	Left	18	−40, −82, −16	19	13.72
Cerebellum					
Lobule V	Left		−16, −52, −22	26	14.04

Table 2

Brain activation foci showing significant differences ($p < 0.001$) between conditions of high and low tactical demand.

Cortical Region	Hemisphere	Brodmann Area	MNI Coordinates	Cluster-level Extent	F value ($F_{1,60}$)
Frontal Lobe					
Middle Frontal Gyrus	Left	8	−26, 26, 50	1119	47.60
Medial Frontal Gyrus	Left	10	−4, 60, 4	372	35.33
Superior Frontal Gyrus	Right	8	20, 36, 48	48	18.69
Paracentral Lobule	Left	5	−2, −44, 60	37	14.11
Parietal Lobe					
Precuneus	Left	31	−4, −52, 32	2961	50.38
Precuneus	Left	7	−22, −76, 48	5563	43.75
Superior Parietal Lobule	Right	7	32, −62, 46	1764	43.27
Temporal Lobe					
Fusiform Gyrus	Left	37	−32, −46, −18	430	33.18
Middle Temporal Gyrus	Right	39	52, −72, 18	895	32.52
Fusiform Gyrus	Right	20	32, −40, −20	207	26.86
Occipital Lobe					
Lingual Gyrus	Left	18	−16, −76, −2	32	15.15
Limbic Lobe					
Hippocampus	Right		30, −18, −18	5	12.84
Cerebellum					
Lobule VI	Right		6, −66, −30	702	29.35
Lobule VI	Left		−20, −66, −38	29	14.99

for the main effect of tactile demand.

The activation foci of effect for the two factors are shown in Tables 3 and 4. For the group effect, significantly higher activations in the primary sensory cortex (BA2), and somatosensory association cortices (BA7) were found in archers compared to non-athletes. In contrast, the primary and secondary visual cortices (BA17, 18), together with medial frontal gyrus (BA6) and the lobule V of the cerebellum, were engaged more in non-athletes than in archers (please see Table 3 and Figs. 2 and 3 for details). As for the effect of sensory demand, significantly higher activations in the secondary visual cortex (BA18), somatosensory association cortex (BA7), and the lobule VI of the cerebellum were found when active discrimination was needed. On the contrary, significantly lower activations during active discrimination were seen in various frontal and temporal areas, including superior/middle frontal gyrus (BA8), medial frontal gyrus (BA10), paracentral lobule (BA5), middle temporal gyrus (BA21, 39) and fusiform gyrus (BA20, 37) (Please see Table 4 and Figs. 4 and 5 for details).

4. Discussion

The purpose of this study was to examine how cerebellar involvement in tactile discrimination differed between people with and without regular sensorimotor training. Contrasting tasks with high sensory demand to those with low sensory demand showed that bilateral associative somatosensory areas (BA7) were engaged more when active tactile discrimination was needed. These findings are in agreement with previous studies suggesting the involvement of associative somatosensory areas for tactile discrimination

Table 3

Location of significant ($p < 0.001$) clusters as shown in Fig. 2.

Cortical Region	Hemisphere	Brodmann Area	MNI Coordinates	Cluster-level Extent	T value (T_{60})
Archers > Non-Athletes					
Parietal Lobe					
Precuneus	Left	7	−20, −82, 46	200	4.51
Postcentral Gyrus	Right	2	50, −32, 36	111	4.08
Inferior Parietal Lobule	Right	40	40, −50, 52	32	3.59
Superior Parietal Lobule	Right	7	20, −70, 56	5	3.39
Non-Athletes > Archers					
Frontal Lobe					
Medial Frontal Gyrus	Left	6	−12, 0, 66	47	3.81
Occipital Lobe					
Lingual Gyrus	Right	17	14, −96, −8	206	4.42
Middle Occipital Gyrus	Left	18	−40, −82, −16	71	3.70
Cuneus	Right	18	2, −90, 18	11	3.44
Cerebellum					
Lobule V	Left		−16, −52, −22	56	3.75

Table 4
Locations of significant ($p < 0.001$) clusters as shown in Fig. 4.

Cortical Region	Hemisphere	Brodmann Area	MNI Coordinates	Cluster-level Extent	T value (T_{60})
HD > LD					
Parietal Lobe					
Superior Parietal Lobule	Right	7	32, −62, 46	2231	6.58
Temporal Lobe					
Fusiform Gyrus	Left	37	−48, −60, −20	8	3.62
Occipital Lobe					
Lingual Gyrus	Left	18	−16, −76, −2	71	3.89
Lingual Gyrus	Left	18	−20, −66, −38	53	3.87
Cerebellum					
Lobule VI	Right		6, −66, −30	832	5.42
Lobule VI	Left		−20, −66, −38	53	3.87
LD > HD					
Frontal Lobe					
Middle Frontal Gyrus	Left	8	−26, 26, 50	1276	6.90
Medial Frontal Gyrus	Left	10	−4, 60, 4	448	5.94
Superior Frontal Gyrus	Right	8	20, 36, 48	69	4.32
Paracentral Lobule	Left	5	−2, −44, 60	112	3.76
Parietal Lobe					
Precuneus	Left	31	−4, −52, 32	3257	7.10
Temporal Lobe					
Fusiform Gyrus	Left	37	−32, −46, −18	495	5.76
Middle Temporal Gyrus	Right	39	52, −72, 18	1193	5.70
Fusiform Gyrus	Right	20	32, −40, −20	288	5.18
Middle Temporal Gyrus	Left	21	−64, −50, −4	9	3.47

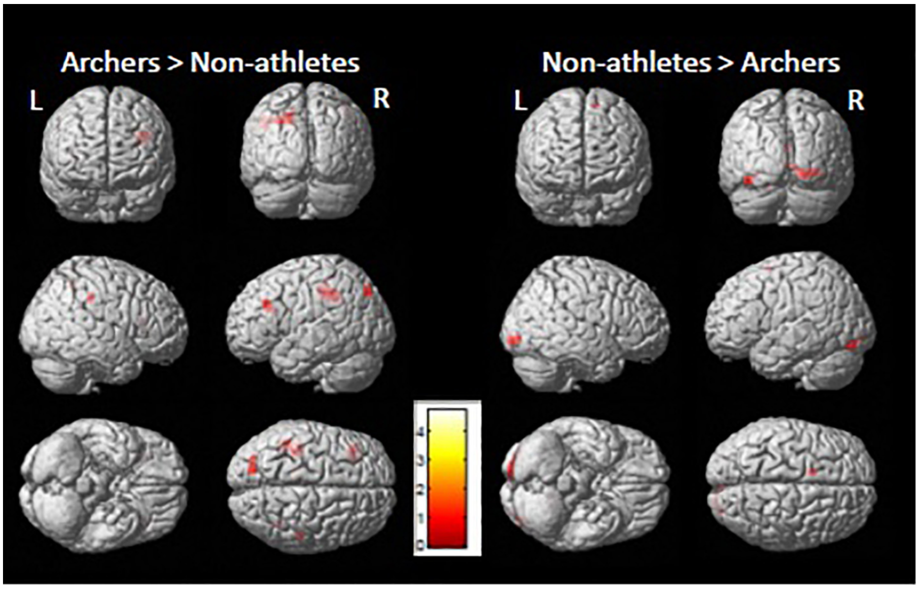

Fig. 2. Brain activation map for the differences between archers and non-athletes.

(Reed, Shoham, & Halgren, 2004; Zhang et al., 2005). Although certain cortical areas yielded higher activities for active tactile discrimination, some other neural substrates showed the opposite activation pattern. It has been suggested that functional deactivations in multiple brain areas, such as the ipsilateral primary somatosensory and motor cortex, supplementary motor area, insula, contralateral cerebellum, and bilateral posterior cingulate cortex, were found during median nerve stimulation. It is suggested that deactivations in these areas are related to altered sensory perception for the contralateral hand during ipsilateral hand stimulation (Klingner et al., 2011). The nature of the relatively smaller activation found in the frontal-temporal areas during active tactile discrimination in the present study is not evident. It may relate to a redistribution of cognitive resources to the most relevant areas during tasks for the efficient organization of brain networks.

Numerous cortical areas showed differential activation patterns between the archers and non-athletic participants. The

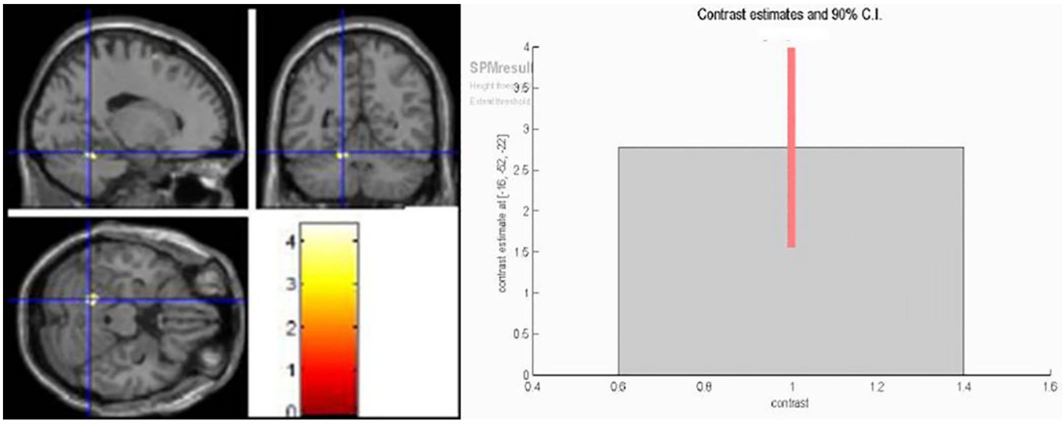

Fig. 3. Significant cerebellar activation and the contrast estimate at (−16, −52, −22) in the non-athletes.

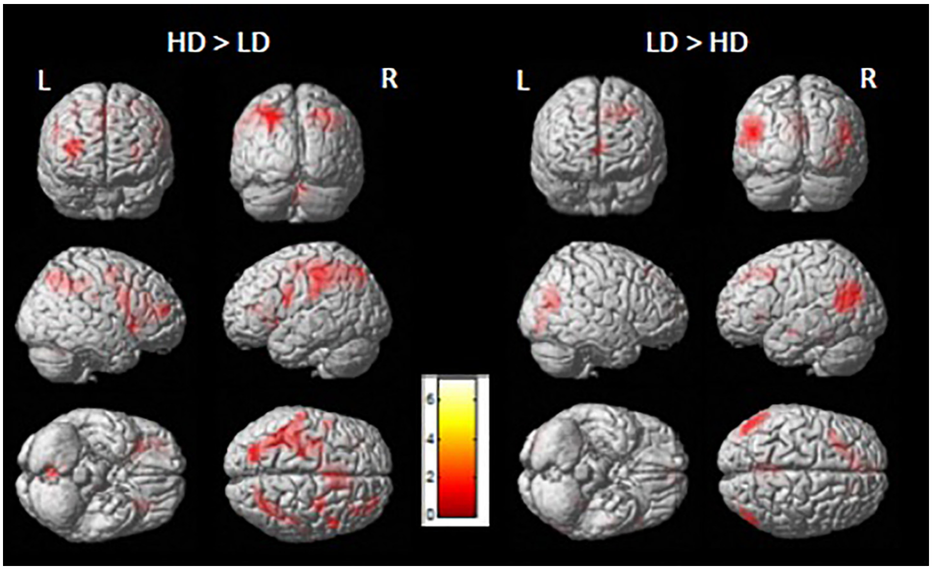

Fig. 4. Brain activation map for the differences of between high and low tactile demand.

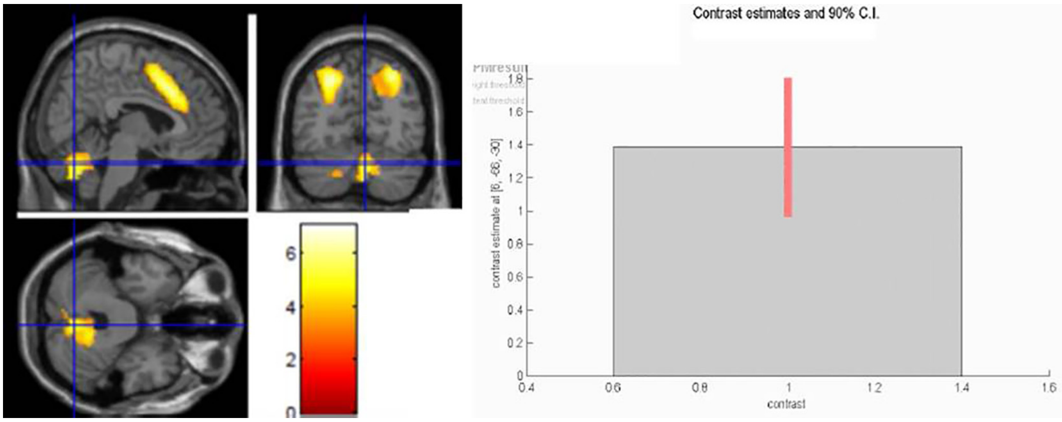

Fig. 5. Significant cerebellar activation and the contrast estimate at (6, −66, −30) for the high tactile demand condition.

supplementary motor area (BA6) was more engaged in the non-athlete participants during the task. This finding may imply that the non-athletic participants need more resources in the planning of their movements to fulfill the task requirements. Some sensory areas were activated more in the archers compared to non-athletes, including the right postcentral gyrus (BA2) and bilateral superior parietal lobule/precuneus (BA7). The sensorimotor task used in the present study required extraction and integration of task-relevant sensory information from multiple modalities. These sensorimotor activations found in archers are arguably related to the efficient linking of sensory and motor information (Zhang et al., 2005).

Apart from the different sensorimotor strategies adopted between archers and non-athletic participants, this study shows that the non-athletic participants recruited the bilateral occipital network (BA17, 18). Visual and tactile modalities are regarded as closely knit because coherent visuotactile perception and visual imagery can be elicited during tactile discrimination (Gentile, Petkova, & Ehrsson, 2011; Nordmark, Pruszynski, & Johansson, 2012; Zhang et al., 2005). The significantly higher occipital activation found in non-athletic participants not seen in the archers may suggest that the former rely more on a strategy of visual imagery to supplement tactile discrimination.

In addition to cortical areas, the lobule V of the cerebellum also yielded significantly higher activation in the non-athletic group than in the archery group. The cortical activation patterns found in the present study suggest that participants without sensorimotor training experience exploit fewer higher-order sensorimotor areas to integrate sensorimotor information. Instead, they adopt a strategy of recruiting more help from the visual cortex for tactile discrimination, which could be argued as an early-stage strategy for sensorimotor learning. Furthermore, it is conceivable that participants in the archery group, after years of sensorimotor training, find the tactile task not as demanding as the non-athletic group. Hence, the higher cerebellar activation for tactile discrimination in the non-athletic group may imply that more sophisticated sensorimotor processing was needed to fulfil the tactile discrimination requirement since the cortical mechanisms for sensorimotor linkage were lacking. This notion is consistent with the finding that the cerebellar lobule V works along with the sensorimotor cortices for overt movement tasks (Stoodley, Valera, & Schmahmann, 2012). In the present study, the difference in sensory demand did not stem from the absolute and objective sensory difficulty of the task, as shown in previous studies (Lee et al., 2005; Molinari & Leggio, 2007; Pastor et al., 2004; Rao et al., 2001; Xiang et al., 2003), but from the relative and subjective sensory difficulty following from distinct sensorimotor experiences. Nonetheless, the present findings still support the cerebellum's role in sensory acquisition by demonstrating higher cerebellar activation for higher sensory demand.

The present findings are also in line with the prediction of cerebellar internal models of motor learning (Imamizu et al., 2000), which posit that diffuse cerebellar activations representing error signals are present during the early stages of motor learning, whereas concise cerebellar activations presenting an acquired internal model will be seen during later stages of motor learning. In contrast to the extensive cerebellar engagements for the non-athletic participants, the lower cerebellar activity in archery athletes may reflect their mastery of an acquired internal model for tactile discrimination after years of archery training. A methodological limitation could not be ruled out in the present study. Although the participants were instructed to match the number of dots, some of them might perform the task by matching the size of the blocks. Future studies are advised to use blocks with equal size or to collect participants' debriefing after the experiment.

5. Conclusion

The present findings confirm the role of the cerebellum in sensory acquisition by comparing the subjective sensory difficulties of people with and without experiences of sensorimotor training. People without experiences of sensorimotor training engage more sensory areas outside the somatosensory cortices in coordination with the cerebellum for tactile discrimination.

Conflict of interest

The authors have declared that no conflicts of interest exist.

Acknowledgements

This research was supported by the Ministry of Science and Technology, Taiwan (NSC100-2314-B-028-002).

References

Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience, 1*, 635–640.

Bower, J. M. (1997). Is the cerebellum sensory for motor's sake, or motor for sensory's sake: The view from the whiskers of a rat? *Progress in Brain Research, 114*, 463–496.

Dum, R. P., & Strick, P. L. (2003). An unfolded map of the cerebellar dentate nucleus and its projections to the cerebral cortex. *Journal of Neurophysiology, 89*, 634–639.

Gao, J. H., Parsons, L. M., Bower, J. M., Xiong, J., Li, J., & Fox, P. T. (1996). Cerebellum implicated in sensory acquisition and discrimination rather than motor control. *Science, 272*, 545–547.

Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). Integration of visual and tactile signals from the hand in the human brain: An FMRI study. *Journal of Neurophysiology, 105*, 910–922.

Imamizu, H., Miyauchi, S., Tamada, T., Sasaki, Y., Takino, R., Putz, B., et al. (2000). Human cerebellar activity reflecting an acquired internal model of a new tool. *Nature, 403*, 192–195.

Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience, 9*, 304–313.

Ivry, R. B., & Keele, S. W. (1989). Timing functions of the cerebellum. *Journal of Cognitive Neuroscience, 1*, 136–152.

Klingner, C. M., Huonker, R., Flemming, S., Hasler, C., Brodoehl, S., Preul, C., et al. (2011). Functional deactivations: Multiple ipsilateral brain areas engaged in the processing of somatosensory information. *Human Brain Mapping, 32*, 127–140.

Kotani, K., Ito, S., Miura, T., & Horii, K. (2007). Evaluating tactile sensitivity adaptation by measuring the differential threshold of archers. *Journal of Physiological Anthropology, 26*, 143–148.

Lee, T. M., Liu, H. L., Hung, K. N., Pu, J., Ng, Y. B., Mak, A. K., et al. (2005). The cerebellum's involvement in the judgment of spatial orientation: A functional magnetic resonance imaging study. *Neuropsychologia, 43*, 1870–1877.

Milton, J., Solodkin, A., Hlustik, P., & Small, S. L. (2007). The mind of expert motor performance is cool and focused. *Neuroimage, 35*, 804–813.

Molinari, M., & Leggio, M. G. (2007). Cerebellar information processing and visuospatial functions. *Cerebellum, 6*, 214–220.

Nordmark, P. F., Pruszynski, J. A., & Johansson, R. S. (2012). BOLD responses to tactile stimuli in visual and auditory cortex depend on the frequency content of stimulation. *Journal of Cognitive Neuroscience, 24*, 2120–2134.

Pastor, M. A., Day, B. L., Macaluso, E., Friston, K. J., & Frackowiak, R. S. (2004). The functional neuroanatomy of temporal discrimination. *Journal of Neuroscience, 24*, 2585–2591.

Petacchi, A., Laird, A. R., Fox, P. T., & Bower, J. M. (2005). Cerebellum and auditory function: An ALE meta-analysis of functional neuroimaging studies. *Human Brain Mapping, 25*, 118–128.

Rao, S. M., Mayer, A. R., & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience, 4*, 317–323.

Reed, C. L., Shoham, S., & Halgren, E. (2004). Neural substrates of tactile object recognition: An fMRI study. *Human Brain Mapping, 21*, 236–246.

Schmahmann, J. D., Doyon, J., McDonald, D., Holmes, C., Lavoie, K., Hurwitz, A. S., et al. (1999). Three-dimensional MRI atlas of the human cerebellum in proportional stereotaxic space. *Neuroimage, 10*, 233–260.

Shih, L. Y., Chen, L. F., Kuo, W. J., Yeh, T. C., Wu, Y. T., Tzeng, O. J., et al. (2009). Sensory acquisition in the cerebellum: An FMRI study of cerebrocerebellar interaction during visual duration discrimination. *Cerebellum, 8*, 116–126.

Shih, L. Y., Yeh, T. C., Kuo, W. J., Tzeng, O. J., & Hsieh, J. C. (2010). Effect of temporal difficulty on cerebrocerebellar interaction during visual duration discrimination. *Behavioral Brain Research, 207*, 155–160.

Stoodley, C. J., & Schmahmann, J. D. (2008). Functional topography in the human cerebellum: A meta-analysis of neuroimaging studies. *Neuroimage*.

Stoodley, C. J., Valera, E. M., & Schmahmann, J. D. (2012). Functional topography of the cerebellum for motor and cognitive tasks: An fMRI study. *Neuroimage, 59*, 1560–1570.

Weaver, A. H. (2005). Reciprocal evolution of the cerebellum and neocortex in fossil humans. *Proceedings of the National Academy of Science USA, 102*, 3576–3580.

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience, 3*(Suppl), 1212–1217.

Xiang, H., Lin, C., Ma, X., Zhang, Z., Bower, J. M., Weng, X., et al. (2003). Involvement of the cerebellum in semantic discrimination: An fMRI study. *Human Brain Mapping, 18*, 208–214.

Zhang, M., Mariola, E., Stilla, R., Stoesz, M., Mao, H., Hu, X., et al. (2005). Tactile discrimination of grating orientation: fMRI activation patterns. *Human Brain Mapping, 25*, 370–377.