Moving tactile stimuli of fingers are integrated in the intraparietal and inferior parietal cortices

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When two cylinders are passively moved in-phase on the volar surface of the right second and third fingers, human subjects estimate the stimuli to originate from one object, whereas two separate objects are estimated for out-of-phase stimuli. While five blindfolded subjects performed this estimation task, brain activity was measured by fMRI. The in-phase stimuli activated the left intraparietal and inferior parietal areas significantly more than did out-of-phase stimuli. These parietal regions may play important roles in the integration of moving tactile stimuli that are independently provided on plural fingers, from which subjects internally construct a single object. *NeuroReport* 14:719–724 © 2003 Lippincott Williams & Wilkins.

Key words: Anterior intraparietal area; Functional magnetic resonance imaging (fMRI); Human; Integration of moving tactile stimuli; Inferior parietal lobe; Primary somatosensory cortex

INTRODUCTION

When an object is moving on two adjacent fingers, the human brain perceives a single object, because a single object provides spatio-temporally consistent stimuli on the fingers. We expect that even when two separate objects are moving on the two fingers, a single object can be perceived if the stimuli have consistent properties, while two objects can be perceived if they are inconsistent in certain properties such as speed or direction. We behaviorally confirmed that a blindfolded human subject could feel a single object when one or two cylinders moved in-phase on the volar surface of the right second and third fingers, while two separated objects were perceived when the two cylinders moved out of phase on the same two fingers.

When perceiving a single object from such spatio-temporally congruent stimuli on separate fingers, tactile information provided from each finger is integrated somewhere in the brain [1,2]. The postcentral gyrus (primary somatosensory cortex and the caudal-most part of the postcentral gyrus, presumably area 2) [3] is known to respond to moving tactile stimuli from non-human primate [2,4–6] and human studies [7,8]. The parietal operculum (PO) was also activated during tactile discrimination of roughness and rotating tactile stimuli in human studies [7,9,10]. The other candidate areas are the posterior parietal regions, which contain neurons responsive to tactile inputs on the hands in area 5 [11], the intraparietal area [12], and area 7 [13]. The posterior parietal regions were also activated when blindfolded subjects explored the shape of an object with tactile inputs [8,10]. For instance, the anterior intraparietal sulcus (aIPS) was active during passive shape discrimination with fingers in a human neuroimaging study [8]. Furthermore, a specific lesion in the left inferior parietal lobule (IPL) impaired two- or three-dimensional shape recognition when the target objects were provided on the right hand [14].

We hypothesized that areas such as the primary somatosensory cortex (SI), postcentral sulcus region, the PO, and the posterior parietal areas could play important roles in the integration of moving tactile stimuli. To test this hypothesis, we measured brain activity using fMRI during a single-object estimation task.

MATERIALS AND METHODS

Subjects: Five right-handed healthy male volunteers aged 23–25 years participated both in the behavioral and fMRI studies. All subjects gave informed written consent approved by the Ethics Committee of Human and Animal Experiments, Kyoto University. None of the volunteers had any history of symptoms requiring neurological, psychological, or other medical care.

Behavioral study: During the behavioral study, the subjects were lying comfortably on a bed in the supine position with their eyes closed, ear-plugged and relaxed. The right arm was stretched and relaxed on a cushion. The palm of the right hand was restrained with adhesive tapes on a sheet

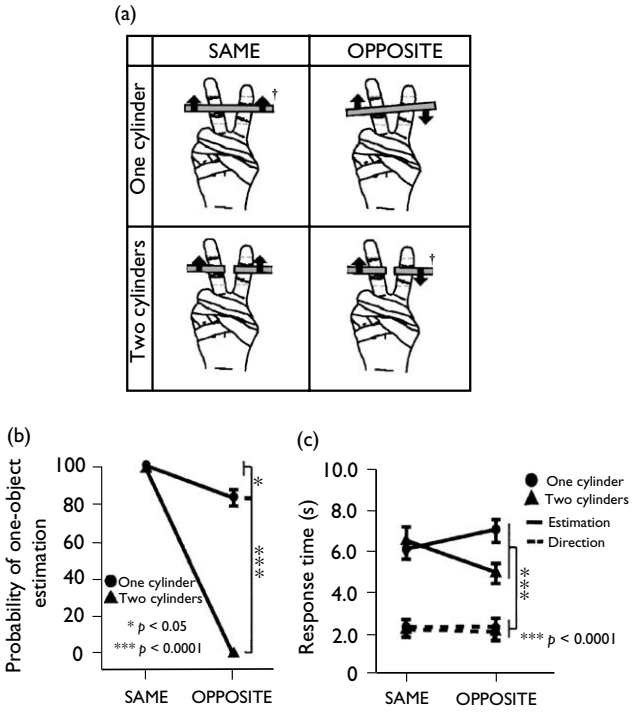

Fig. 1. (**a**) Task conditions for the estimation task in the behavioral study. A cylinder periodically moved on the fingers in the same phase (one-same condition) or in the opposite phase (one-opposite), while the two cylinders moved in the same phase (two-same) or in the opposite phase (two-opposite). Symbols (†) in the figure indicate the conditions selected for the fMRI experiments. (**b**) Mean probability estimation for one object during the estimation task (with s.e.m.). In the one-opposite condition, the subjects occasionally showed two-object estimation. Asterisks indicate the significant level between conditions. (**c**) The response time for the direction task was significantly lower than that for the estimation task.

of polystyrene foam to make a shape like a peace sign, so that the stimuli were moved exactly on the target areas on the second and third fingers and did not touch any other part of the right hand (Fig. 1a). A well-trained experimenter manually applied tactile stimuli to those fingers as consistently as possible.

Wooden cylinders (about 11.0 cm long; 1.0 cm diameter; 10.0 g) with smooth surfaces were used as stimuli on the skin. The subjects did not see the stimuli and were not even informed about the type of stimuli until the entire experiment was over. The stimuli were applied to the volar surfaces of the distal and proximal interphalangeal joints of the indicated fingers (Fig. 1a). The borders of stimulation were demarcated with black ink in advance and the displacement length was ~4 cm along the middle phalanx. The cylinders were periodically moved along the bone within the demarcated zones and auditorily paced at 0.3 Hz. The movement of the stimuli was recorded on a digital video recorder (GV-D900 NTSC mini DV and CCD-MC100, Sony Corporation, Tokyo, Japan). The averaged speed of the moving stimuli for each subject was calculated for each trial in all subjects. We carefully avoided excessive pressure to allow the cylinder to move smoothly on the skin.

Estimation task: The subjects participated in four conditions in order to clarify the most critical factor for perceiving a single object from the second and third fingers (Fig. 1a). One cylinder moved periodically on the index and middle fingers in the same phase (one-same condition) and was semi-rotated in the opposite phase (one-opposite condition). Two identical cylinders also moved periodically proximal to the distal, or *vice versa*, in the same phase (two-same condition), or in the opposite phase (two-opposite condition). The average speeds of stimuli in the four conditions were very similar (2.36 ± 0.03 cm/s, one-same; 2.36 ± 0.03, one-opposite; 2.42 ± 0.02, two-same; 2.39 ± 0.03, two-opposite; mean $\pm$ s.e.m.).

During each trial, the subjects were asked to say 'yes' as soon as they were certain the stimuli originated from one object or two. This vocal reply provided the response timing when they were certain. After stimulation for 15 s, the subjects answered either 'one' or 'two' and also rated the clarity of estimation in 10-grade scales (from 0, for two-object estimation, to 10, for one-object estimation). Each condition was repeated 20 times in a pseudo-randomized order. The tactile stimuli always started moving from the middle of the stimulated skin area in each trial.

Direction task: In this task, they were instructed to simply judge whether the stimuli on their fingers moved in the same phase or in the opposite phase. The subjects also said 'yes' as soon as they were certain. Each stimulation was terminated when the subject said 'yes'.

fMRI study: The two conditions that showed the highest probability for estimating one object (one-same) or two objects (two-opposite) were selected from the four stimuli in the behavioral task. For control conditions, either the second or third finger was separately stimulated (single condition). The average speeds of the stimuli were almost the same (2.90 cm/s) across the three conditions. The one-same, two-opposite and single conditions for each finger were repeated three times in each session. Each task condition was alternated with a baseline condition in which no tactile stimuli were provided. The order of the conditions was randomized across subjects. Each condition lasted for 30 s (TR = 6 s: five functional images were collected). Eventually, 15 functional images were collected for one condition per subject. Each condition was followed by a resting period of 30 s.

The subjects were instructed to stay relaxed during the experiment and not to make any overt movement of the fingers. In the one-same and two-opposite conditions, the subjects were asked to estimate whether the moving stimuli originated from one or two cylinders. During the single condition the subjects received the stimuli passively. They were not allowed to make any kinds of response during the fMRI experiment; instead, the subjects performed the two (one-same and two-opposite) conditions from the behavioral task with a verbal response three times both before and after the fMRI experiment. The subjects could precisely estimate whether the stimuli originated from one or two cylinders during the scanning, as was the case in the behavioral task.

Data acquisition and processing: fMR images were acquired on a 1.5 T scanning system (Magnex Eclipse 1.5 T Power Drive 250, Shimadzu Marchoni). The functional images consisted of fifty consecutive slices. A T2*-weighted gradient EPI sequence was used (TR/TE = 6000/60ms; FA = 90°; voxel size = 3 × 3 × 3 mm). Before the acquisition of functional images, T2-weighted anatomical images were obtained in the same plane as the functional images (voxel size = 0.75 × 0.75 × 3 mm). Additional T1-weighted high-resolution anatomical images (voxel size 1 × 1 × 1 mm) were also obtained.

Image processing and statistical analysis were performed with the Statistical Parametric Mapping package SPM99 implemented in MATLAB (Mathworks Inc., Sherborn MA, USA) [15–17]. Firstly, functional images from each run were realigned to the first scan. Then, the T2-weighted anatomical images were co-registered to the first scan in the functional images. Each co-registered T2-weighted anatomical image was normalized to a standard T2 template image as defined by the Montreal Neurological Institute (MNI). The parameters from this normalization process were then applied to each functional image. Finally, these spatially normalized functional images were re-sampled to a voxel size of 2 × 2 × 2 mm and smoothed using a 10 mm FWHM Gaussian kernel. High-resolution anatomical images were also normalized by the same procedure.

Data were analyzed by the General Linear Model approach [15]. The time series for each voxel was high-pass filtered to 1/120 Hz and low-pass filtered by a canonical hemodynamic response function. Global signal changes were removed by scaling. The task-related neural activities for each condition were modeled with a box-car function convoluted with a canonical hemodynamic response function. To test the hypotheses for region-specific condition effects, linear contrasts were employed. The contrast of the one-same *vs* a baseline condition was used to examine brain regions activated solely by the one-same condition. Then, contrasts of the one-same *vs* two-opposite and the two-opposite *vs* one-same were examined to compare the differences between the one-same and the two-opposite conditions. The resulting SPM{T} for these contrasts were thresholded at $t(509.6) = 3.11$ ($p < 0.001$ uncorrected for multiple comparisons). Voxels that did not reach a significant level ($p < 0.001$ uncorrected) when the one-same was contrasted with a baseline condition were excluded. We reported the brain regions with a significant $p < 0.05$ cluster level corrected for multiple comparisons over the whole brain. We used identical procedures to identify the active fields in the two-opposite *vs* one-same condition.

The anatomical localization was assessed by superimposition of the SPM{T} on the group mean MR image [18]. The volume of interest (VOI) was defined as a sphere with a 10 mm radius at the center of the peak voxel in each cluster in the contrast of the one-same with the baseline condition. Percent signal increase was defined as the mean percentage of the BOLD signal change in each condition divided by that in the baseline condition. First scans from each epoch in each condition were excluded from this analysis. Percent signal increase in each VOI was statistically evaluated between the conditions (one-same, two-opposite, and single conditions) by ANOVA with the SPSS software package (Version 10.0J, SPSS Japan Inc., Tokyo Japan).

RESULTS

Estimation task: Fig. 1b shows the probability of the one-cylinder estimation for the stimuli given to the subject. When the stimuli moved in-phase, the subjects clearly estimated that the stimuli originated from one cylinder, regardless of whether one (one-same) or two cylinders (two-same) moved (rate of clarity, 9.7 ± 0.2 for one-same; 9.3 ± 0.4 for two-same). They sensed a long obscure object moving on both the second and third fingers in both conditions. The subjects needed significantly more time (4 s) to estimate the number of objects than when they simply judged the direction of moving phases (Fig. 1c).

When the stimuli moved out-of-phase, the probability of one-cylinder estimation became lower than when the stimuli moved in-phase (Fig. 1b). The subjects mis-estimated ~20% of all trials in the one-opposite condition and showed more ambiguous clarity of estimation (6.7 ± 0.7). However, the subjects precisely estimated that the stimuli originated from two cylinders in the two-opposite condition (0.4 ± 0.4). In the one-opposite condition, the subjects reported that a long object was periodically swinging on the fingers when they estimated one object. Two-way ANOVA (2 phases (same, opposite) × 2 stimuli (one-cylinder, two cylinders)) of probability showed a significant interaction between the two factors ($F(1,4) = 206.6$, $p < 0.001$). A paired *t*-test showed a significant difference in the probability between the two-opposite and other conditions ($df = 4$, $t = 99.0$, $p < 0.0001$, two-same; $df = 4$, $t = 15.7$, $p < 0.0001$, one-opposite). Significant differences were also observed between the one-opposite and one-same ($p < 0.05$), and between the one-opposite and two-same conditions ($p < 0.05$).

These results show that the subjects estimated one cylinder when the stimuli were moving in-phase, regardless of whether one or two cylinders were actually moved. On the contrary, the subjects could precisely estimate that the stimuli originated from two cylinders when two cylinders were moving out of phase. These results suggest that the phases of stimulation on the fingers, but not the number of cylinders, might be an important factor when perceiving a single object.

Direction task: All subjects needed more time for the object estimation in all four conditions than for the direction judgment (Fig. 1c). When the subjects judged the direction, the response time was the same among the conditions. A three-way ANOVA (2 tasks (estimation, direction) × 2 stimuli (one cylinder, two cylinders) × 2 phases (same, opposite)) of response time showed a significant difference between the tasks ($F(1,4) = 52.5$, $p < 0.01$). This result clearly show that the subjects estimated whether the stimuli originated from one or two objects not by simply judging the direction of the moving stimuli.

fMRI results: The two conditions selected from the four behavioral conditions (one-same and two-opposite conditions) were matched in task demands such as response time and probability (Fig. 1b,c). Table 1 shows the significantly active areas when the one-same was contrasted with a baseline or the two-opposite condition. Compared with the baseline, three significant clusters were activated (Fig. 2).

Table I. Significantly activated voxels in the contrasts comparing the one-same to a baseline and to the two-opposite condition.

Anatomical region	x	y	z	t(509.6)
One-same *vs* baseline				
Left hemisphere				
Primary somatosensory cortex (SI)	−40	−18	58	12.8
Parietal operculum (PO)	−44	−24	22	6.98
Anterior intraparietal sulcus (aIPS)	−42	−50	34	5.55
Inferior parietal lobule (IPL)	−54	−58	28	4.37
Right hemisphere				
Cerebellum, anterior lobe	20	−54	−20	6.36
One-same *vs* two-opposite				
Left hemisphere				
Anterior intraparietal sulcus (aIPS)	−40	−48	32	4.95
Inferior parietal lobule (IPL)	−54	−58	24	4.57

x, y, z are stereotaxic coordinates (mm); t scores are peak activations within a significant cluster of activated voxels; $t(509.6) > 3.11$ corresponds to $p < 0.001$ (uncorrected for multiple comparisons). There was no significantly activated region in the contrast of the two-opposite *vs* one-same condition.

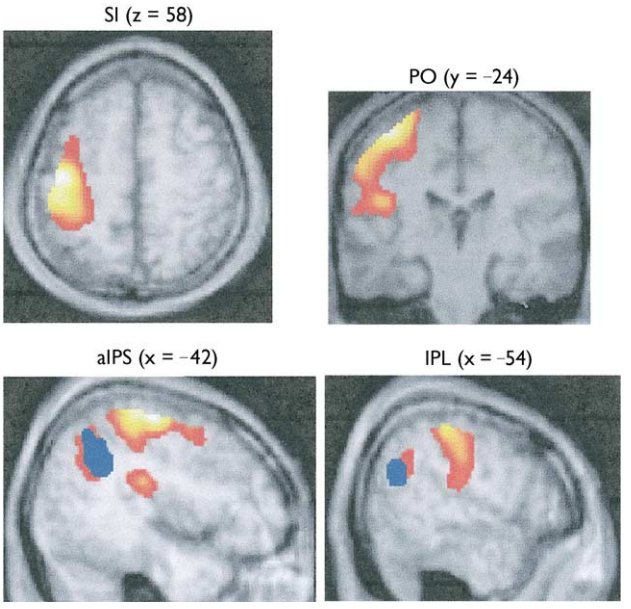

Fig. 2. Significantly activated regions in the contrasts of the one-same *vs* a baseline condition. Horizontal section at $z = 58$ for the primary somatosensory cortex (SI) and caudal-most part of postcentral gyrus (area 2), coronal section at $y = -24$ for the parietal operculum (PO) and sagittal section at $x = -42$ for the anterior intraparietal sulcus (aIPS) and at $x = -54$ for the inferior parietal lobule (IPL). Blue areas were identical sections that were also significantly activated in the contrast of the one-same *vs* two-opposite conditions.

One cluster was located in the contralateral (left) primary somatosensory area (SI), extending rostrally into the dorsal premotor cortex, dorsally into the superior parietal lobe and inferiorly into the parietal operculum (PO). The second cluster was located in the ipsilateral anterior lobe of the cerebellum. The last cluster was located in the contralateral anterior part of the intraparietal sulcus (aIPS), extending superiorly in the superior parietal lobe and inferiorly into the inferior parietal lobule (IPL).

When the one-same was compared with the two-opposite condition, two peaks of significant activation were found in the cluster. One peak was located deep in the aIPS, and the second in the IPL (Fig. 2). No conspicuous clusters were identified in the postcentral gyrus. The contrast of the two-opposite *vs* one-same did not show any significant activation.

Fig. 3 shows the mean percentage increase of BOLD signals in the peaks of the one-same condition compared with the baseline. The peaks in the SI and PO showed higher activities in the one-same and two-opposite than in the single conditions. One-way ANOVA (3 conditions (one-same, two-opposite and single conditions) of the mean percentage increase showed a significant difference among the three conditions in the SI ($F(2,8) = 6.0$, $p < 0.05$) and PO ($p < 0.05$). Tukey's HSD test for multiple comparisons showed significant differences between the two-opposite and single conditions in both regions ($p < 0.05$, both). On the contrary, the peaks showed significantly higher activities in the one-same among the three conditions in the aIPS ($F(2,8) = 18.0$, $p < 0.001$ for ANOVA and $p < 0.01$ for multiple comparisons) and IPL ($F(2,8) = 6.2$, $p < 0.05$ for ANOVA and $p < 0.05$ for multiple comparisons), confirming the significant difference in brain activities in the aIPS and IPL revealed by the contrast of one-same *vs* two-opposite.

DISCUSSION

The present results show that intraparietal and inferior parietal cortices were active when blindfolded subjects estimated whether they received tactile stimuli originating from a single object or two discrete ones. The contrast of one-same *vs* two-opposite conditions revealed brain activities specific for integration of in-phase moving stimuli on two fingers, as the speed of the tactile stimuli and stimulated areas were controlled to match for these conditions. Thus, we conclude these parietal regions may play important roles in tactile perception for a single object from moving stimuli that are independently provided on plural fingers.

The anterior intraparietal sulcus and inferior parietal lobule for the integration of tactile stimuli on fingers: Our original hypothesis was that the anterior primary somatosensory cortex (SI), the caudalmost part of the postcentral gyrus (area 2) and parietal operculum (PO) might be involved in the integration of moving tactile stimuli when a subject perceives a single object. This hypothesis derives from evidence that convergence of tactile inputs from plural fingers occurred in the SI and area 2 in non-human primates [2,5]. For instance, receptive fields in area 3b included small parts of the fingers, while multidigit representation is seen in area 1 and even bimanual representation in area 2. Our results are in good agreement with this evidence, as activities in the SI and area 2 (and the PO) were higher in simultaneous tactile stimulation of the fingers than individual tactile stimulation on each finger. Furthermore, from the convergence of tactile inputs in the SI and area 2, we can assume that the primary somatosensory regions also perceptually integrate tactile inputs from fingers. However, the present study showed no conspicuous difference in

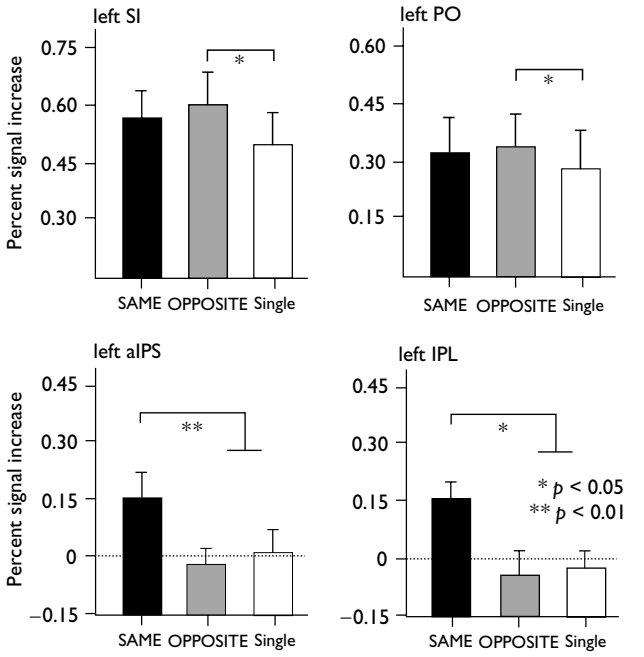

Fig. 3. The volume of interest (VOI) was defined as a sphere with a 10 mm radius at the center of the peak voxel in each cluster in the contrast of the one-same with the baseline condition. The mean percentage increases in the BOLD signal in each area for each task condition are shown with s.e.m. In the primary somatosensory cortex (SI) and parietal operculum (PO), the mean percent increase did not show a significant difference between the one-same (same in the figure) and two-opposite (opposite) conditions, while the one-same was the highest among the conditions in the anterior parietal sulcus (aIPS; $F(2, 8) = 18.0$, $p < 0.001$) and inferior parietal lobule (IPL; $F(2,8) = 6.2$, $p < 0.05$). Asterisks indicate the significant level between conditions.

brain activity between in-phase and out-of-phase stimulation on the two fingers in these areas; in other words, these regions might respond equally to plural tactile stimulation, regardless of single-object perception. This result suggests that these primary areas are important for processing moving tactile stimuli, but not crucial for perceptually integrating tactile inputs from fingers.

Therefore, is there any additional region needed for single-object perception? Our results illustrate that posterior parietal regions are involved in perceptual integration of tactile stimuli as a single object. Posterior parietal regions have several areas responsive to tactile inputs on hands in non-human primates [11–13]. Directional tactile motion on a monkey's hand activated area 5 [11] and area 7 [13]. This evidence alone, however, cannot explain the lack of significant activity in the posterior parietal region when tactile motion was provided on single fingers in the present study (Fig. 3). The posterior parietal areas were also active in previous studies on tactile shape discrimination. The anterior intraparietal region was specifically activated when human subjects explored objects with plural fingers for shape discrimination [8,10,19]. The inferior parietal region was also activated when subjects manipulated and identified an object's shape with several fingers [20]. Furthermore, Reed *et al.* showed that a patient with a focal lesion in the left inferior parietal area failed to haptically perceive object shapes with the right hand [14]. This perceptual impairment might be caused by a dysfunction of tactile integration from the fingers to perceive an object's shape. When the shape of an object was tactually explored in these studies, the brain first needed tactile information from the fingers, so that the synthesis of tactile information needed to compute the spatial profile of an object could occur. The posterior parietal regions are not active in texture discrimination, when the integration of tactile inputs from fingers is not strongly required [8,10]. This assumption is also supported by the fact that the posterior parietal areas may play a central role in transformation of spatial representations for multiple sensory modalities [21,22]. One may speculate that this parietal region was activated to transform the somatotopic representation of tactile motion to a spatial representation for tactile shape perception. Thus, it is reasonable to assume that not only the primary areas, but also additional regions in the posterior parietal region, need to be recruited when the spatial profile of the tactile information is integrated from the fingers. We conclude that these parietal regions may play important roles in tactile perception for a single object from moving stimuli that are independently provided on multiple fingers.

CONCLUSION

When moving stimuli were provided in-phase on separate fingers, the subjects estimated that the stimuli originated from one cylinder, regardless of whether one or two cylinders actually moved. The posterior parietal regions, but not primary sensory cortices, might play important roles in integration of moving tactile stimuli when subjects estimate single objects from moving stimuli that are independently provided on fingers.

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