Abstract  Tools are often compared to a part of our own “body”. Since the end of the 20th century, neuroscientists and psychologists have accumulated evidence suggesting that the “tool as a part of the body” is not just a metaphor, but is a fact in the brain. In the introduction of this article, we review a neurophysiological study on the monkey brain that achieved a breakthrough in this area of research. Subsequently, we review studies in humans. In the first section, we explain the psychophysical studies that suggest the perceptual assimilation of tools and hands and neuroimaging reports regarding the neural correlates of perceptual tool-hand assimilation. In the second section, we describe the spatial action capability with tools or extracorporeal objects based on behavioral studies regarding locomotion, such as load-carriage and wheelchair-use. Based on these findings, we discuss current and future research issues regarding the tool-body interaction in the context of neural mechanisms and applications.

Keywords: tool-use, body schema, brain, illusion, locomotion, wheelchair-use

Introduction

Dexterous utilization of tools, along with bipedal locomotion and language, can be considered a behavior that characterizes human beings. Tools have helped develop our behavior, life, technology, and culture. Favorite tools are often compared to a part of our own “body”. At the end of the 20th century, a neurophysiological study on the monkey brain revealed that the “tool as a part of the body” is not just a metaphor, but is a fact in the brain.

Iriki et al. (1996) investigated neuronal activity in the intraparietal cortex (IPS; see Fig. 1A) of Japanese monkeys that were trained to use a tool. The Japanese monkeys could use a rake to pull foods closer after two weeks of training. The use of the rake enabled the monkeys to reach the distant food. That is, the tool extended their reaching distance. In the IPS, Iriki et al. recorded single-neuron activity from bimodal neurons that responded both to somatosensory stimuli from a body region (i.e., somatosensory receptive field, sRF; Fig. 1B) and to visual stimuli from space (visual receptive field, vRF; Fig. 1C). The vRF was anchored to the body part. For example, when the hand was moved, the vRF followed the sRF. Iriki et al. found that after the monkeys learned to use the rake, the vRFs of the bimodal neurons in the IPS expanded to include the whole length of the rake (Fig. 1D). By contrast, the expansion of the vRFs did not occur when the monkeys were only passively holding the rake (Fig. 1E). This finding strongly suggested that the neural representation of the body was extended as if assimilating the tool into the body.

This finding in the monkey brain inspired studies in humans in the current century, which have resulted in psychological and neuroscientific evidence for tool-body assimilation. In the first section of this article, we review the psychophysical and neuroimaging findings on the perceptual assimilation of tools and hands. In the second section, we review behavioral findings on locomotion with tools or extracorporeal objects, such as load carriage and wheelchair use, to extend our perspectives to dynamic whole body behavior in our environment.

1. Perceptual assimilation of tools and hands

I) Crossed-arm deficit in tool use

With ordinal postures of the arms (e.g., uncrossed arms, Fig. 2A), individuals can correctly perform temporal order judgment (TOJ) between two successive tactile stimuli across the hands, with intervals as short as 70 ms. However, when the individuals cross their arms (Fig. 2B), the misreporting of TOJ increases with moderately short intervals (< 300 ms). This crossed-arm deficit in TOJ suggests that the brain processes the spatial locations of the hands before temporally ordering the tactile signals from the respective hands. Yamamoto and Kitazawa (2001b) subsequently investigated TOJ of two successive stimuli delivered to the tips of drum sticks held in
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When both sticks and arms were uncrossed (Fig. 2C), the participants correctly performed TOJ. When the arms were crossed with the sticks uncrossed (Fig. 2D), the number of misreported TOJs increased. These results are consistent with previous reports of the crossed-arm deficit in TOJs of tactile stimuli directly delivered to the hands. Importantly, when the sticks were crossed with the arms uncrossed (Fig. 2E), the number of misreported TOJs also increased. Therefore, a crossed-“stick” deficit occurred in TOJ. Furthermore, when both sticks and arms were crossed (Fig. 2F), the participants correctly performed TOJ confirming that the crossed-stick deficit was not simply due to the complex configuration of the sticks and arms. Thus, the brain processes the temporal order of the stimuli to the tips of the sticks as if the sticks are assimilated into the hands.

2) Neural correlates of hand-object illusion

Naito and Ehrsson (2006) conducted functional brain imaging (fMRI) to identify the neural correlates of perceptual hand-object interaction using a somatosensory illusion. Vibrating the tendon of the limb elicits a kinesthetic illusion. For example, when the tendon of the wrist extensor muscle is vibrated, the participants perceive illusory passive flexion of the wrist (Fig. 3A). Naito and Ehrsson ingeniously developed the illusion. When the participants touched the surface of a ball, vibrating the tendon of the wrist extensor muscle elicits an illusion that the touched ball is moving along with the illusory wrist.
flexion (hand-object illusion, Fig. 3B).

Naito and Ehrsson identified the neural correlate of the hand-object illusion in the left inferior parietal lobule (IPL, see Fig. 4). Based on this result, the authors suggested a parietal mechanism that links an external object with our own hand when the object or tool becomes assimilated into our body representation. This finding is generally consistent with the results from the single-neuron recordings in the monkey brain\(^9\).

Furthermore, the same research group reported the neural correlates of the perceptual hand-object interaction using a bimanual version of the hand-object illusion\(^8\). In this study, participants held a cylinder between the palms of their two hands. Under this condition, while vibrating the tendon of the right wrist extensor muscle, the participants perceived the illusion that the cylinder was shrinking from the right side along with illusory passive flexion of the right wrist (Fig. 5B). The fMRI results revealed that the bimanual shrinking-object illusion activated anterior parts of the superior parietal lobule (SPL, see Fig. 4) bilaterally and the left IPL and Brodmann’s area (BA) 2 (i.e., part of the primary somatosensory cortex, S1). In their previous report\(^6\), the left IPL was a neural correlate of the illusory unimanual hand-object interaction. Based on the observations, the authors proposed a hierarchical organization of somatic perception of hand-object interactions in the parietal structure. That is, in addition to the left IPL, the bilateral anterior SPL was also involved when estimating the spatial relationship between the two hands and a hand-held object.

3) Cutaneous rabbit, somatotopic illusion extends to a stick held by the hands

Miyazaki et al. (2010)\(^9\) focused on a classical somatosensory illusion called the “cutaneous rabbit”\(^10\). When a series of rapid taps are delivered first at one location on the skin and then at another without a break in regularity, the recipient perceives illusory taps between the actual stimulation locations as if a small rabbit were hopping along the skin between the two sites. The cutaneous rabbit illusion has attracted interest not only from neurosci-
entists and psychologists, but also from philosophers because the illusion is considered to be evidence for “postdiction.” The perceptual retroactive effect becomes clearer in the simplified version of the illusion. As shown in Fig. 6, individuals receive three successive mechanical pulses (P1, P2, and P3) on the forearm. P1 and P2 are delivered at one site, and P3 is delivered at another site on the forearm. The time interval between P1 and P2 is moderately long (e.g., 800 ms), whereas the time interval between P2 and P3 is short (e.g., <100 ms). Then, the individuals perceive P1 at the actual stimulus site, but perceive P2 and P3 at illusory sites that are spatially close to each other on the forearm. Thus, the relatively future event, P3, affects the perception of the past event, P2.

Miyazaki et al. (2010) applied similar tactile stimuli to both index fingers of the participants. When the participants received the stimuli via small plates with each plate placed on each index finger pad, all of the stimuli were perceived at the actual stimulus sites (Figs. 7A and B). However, when the participants held a stick between the index fingers and attended to the whole stick, the tactile stimuli via the stick elicited the cutaneous rabbit sensation along the stick (Figs. 7C and D).

The finding of the cutaneous rabbit illusion on the stick raises a question(s) concerning the neural mechanism of the cutaneous rabbit effect and/or tool-body interaction.

Fig. 6 Cutaneous rabbit illusion (simplified version). P1, P2, and P3 represent the first, second, and third mechanical pulses, respectively, that provide tactile sensations to the participant’s forearm. P2 and P3, presented at a short time interval (e.g., <100 ms), are perceived at illusory skin sites that are spatially close to each other.

Fig. 7 Cutaneous rabbit illusion hopping along the stick held by the hands. Tactile stimuli similar to Fig. 6 (P2-P3 time interval = 50 ms or 80 ms) were applied to both index fingers of the participants. (A) Under the no-stick condition, all of the stimuli were perceived at the actual stimulus sites. (B) Mean values across participants of the deviation of the reported stimulus sites from the actual sites for the no-stick condition. (C) Under the stick-holding condition, the cutaneous rabbit sensation occurred along the stick. (D) Mean values across participants of the deviation of the reported stimulus sites for the stick-holding condition. The small plates (A) and stick (C) were made of aluminum with an identical thickness. This figure was adapted from Miyazaki et al. (2010).
An fMRI study\(^{(3)}\) reported that the illusion involves somatotopic activity in S1 (BA 1). That is, when participants felt the cutaneous rabbit illusion, neural activation was observed in the S1 region that corresponded to the skin site where the illusory sensation occurred. The cutaneous rabbit illusion is thus associated with the early sensory body map representation in S1. This association is exactly in accordance with the notion of tool-body assimilation in the brain. However, according to the standard knowledge of physiology, S1 represents only our own body and should not represent external objects/tools\(^{(16)}\). Moreover, the preceding studies described above focused on the posterior parietal cortex (PPC) that includes the IPL, IPS, and SPL as the neural correlates of the objects/tools interacting with the body. Meanwhile, the neural correlates of the cutaneous rabbit illusion were not observed in the PPC at all\(^{(15)}\). Accordingly, we must update physiological knowledge on the cutaneous rabbit effect and/or tool-body interaction. At this stage, we can propose two possible mechanisms.

A more probable mechanism is consistent with the idea of the hierarchical organization of the somatic perception of hand-object interaction\(^{(8)}\). Specifically, when individuals hold an external object/tool, the cutaneous rabbit effect additionally involves the PPC. In addition to S1, the neural correlates for the cutaneous rabbit illusion are also observed in the right premotor cortex (PMC) and dorsolateral prefrontal cortex, and these areas are assumed to be involved in top-down modulation of somatosensory integrative processing in S1 to generate the cutaneous rabbit effect\(^{(15)}\). The PMC constructs functional connections with the PPC in relation to body-space representation\(^{17,18}\). Observation of tools activates the parietal–premotor circuit\(^{(3)}\). The PMC and PPC (intraparietal cortex) were reported as neural correlates of the somatic rubber-hand illusion\(^{(20)}\). Top-down modulation by the PMC may operate higher somatosensory integrative processing in the PPC when individuals are holding an external object/tool.

We cannot exclude the possibility of the essential involvement of S1 in perceptual tool-body interaction. An fMRI study\(^{(21)}\) demonstrated that the activity of the primary sensorimotor area, including S1 (BA 3/BA 1), increased during the bimanual manipulation of an object. In this task, interactions between the hands should be transmitted via the object. Thus, the brain should take into account the property or dynamics of the object to perform the task. The observation by Theorin et al. (2007)\(^{(21)}\) might reflect some transient plasticity in S1 according to object handling. In Naito et al. (2008)\(^{(8)}\), S1 was observed as one of the neural correlates of the perceptual hand-object interaction, although there were detailed differences in BA (1 in Blakeburg et al. 2006\(^{(15)}\); 2 in Naito et al. 2008\(^{(8)}\)). Humans are constantly handling a variety of tools. It may be a small wonder that the human’s S1 has evolved to enable some plasticity for tool-use. Of course, these hypotheses are merely speculative. To advance the discussion, we have to wait for future neurophysiological and/or neuro-imaging evidence.

2. Tool-body assimilation during human locomotion

1) Representation of space in response to altered action capabilities is critical during locomotion

In the previous section, we demonstrated that when one is wielding a stick, the stick is perceptually assimilated into the body as if it were an extension of the body\(^{(1,5,6,8,9)}\). In fact, the body schema can cover extracorporeal (i.e., not related to the body) objects that are in contact with or in close proximity to the body, such as clothes, rings, or tools\(^{(22,23)}\). The use of a hand-held stick extends one’s reach. As a result, the representation of space is also modified in response to action capabilities altered by a hand-held stick.

How accurately the brain modifies the representation of space in response to altered action capabilities with tools or other extracorporeal objects is critical, particularly for achieving safe locomotion. For instance, the use of locomotion-assistance devices, such as wheelchairs or walkers, enhances the mobility of older individuals or individuals with lower-limb disabilities. The use of these devices, however, also results in the individual’s inability to pass through narrow apertures because of the width of the devices and biomechanical movement constraints (Fig. 8). Action capabilities are also altered when individuals

Fig. 8  Examples of locomotion with extensions. Representing an external object as if it were a biological extension of the body and accurate representation of space in relation to the body-plus-object is necessary to achieve safe locomotion without collision.
walk while holding a shopping bag or a large box. In this case, a wider space than usual is transiently necessary for locomotion. Therefore, not only must an individual represent an external object as if it were a biological extension of the body, the accurate representation of space in relation to the body-plus-object is also necessary to achieve safe locomotion without collision.

In this section, we review a number of relevant studies demonstrating how accurately space is perceived in response to altered action capabilities with a tool or other extracorporeal objects. The summary of these studies will yield several tentative conclusions: (a) adaptation to altered action capabilities is very quick, at least when the form of locomotion is well-learned; (b) it would take a long time to adapt to altered action capabilities when individuals use unfamiliar forms of locomotion; (c) visual information necessary for representing space in relation to a person-plus-object is different depending on whether the locomotion form is well-learned or not; and (d) practice performing a given behavior (direct practice) is unlikely to be necessary to quickly adapt to altered action capabilities and to perceive the space required for that behavior.

2) Rapid adaptation to altered bodily states when using a familiar form of locomotion

Individuals can maintain their normal locomotor patterns in space with the addition of mass either to one limb24) or to the trunk25). This evidence demonstrates the adaptability of the brain to altered action capabilities. In fact, the adaptation is very quick when the form of locomotion is well learned.

When walking through an aperture, individuals generally rotate their body when an opening is narrower than 1.1-1.3 times their shoulder width26,27). Several studies have demonstrated an individual’s superior ability to adapt to artificial extensions of body dimensions and select appropriate behavior for walking through an aperture without collision28-32). In one study28), young individuals were asked to walk through a narrow aperture while holding a long horizontal bar that required a space of approximately 20 cm wider than that required for normal walking (Fig. 9). The results indicated that they adapted very successfully. Virtually the same locomotor patterns used for normal walking were produced, and no collisions occurred. A subsequent study demonstrated that even while holding a bar, the brain controls the behavior of walking through apertures based on this rule: the amplitude of body rotation needed to ensure that the minimal spatial margin is created at one side of the body (i.e., a space of 6-8 cm was created between the door edge and the body) at the time of crossing29).

Pregnant women also demonstrate adaptability to their changing bodily states over the course of pregnancy31). In this study, their judgment accuracy for their minimum passable width with body rotation was measured over the course of pregnancy. The results indicated that pregnant women tracked their changes in their minimum passable width. Their accuracy was nearly equivalent to that of non-pregnant, control participants.

Furthermore, tetraplegic patients who were experienced with wheelchair use demonstrated their enhanced ability to estimate the space required for locomotion with both familiar and unfamiliar wheelchairs33). Tetraplegic patients generally lacked somatosensory input from the upper limbs and were unable to obtain information about the dimensions of a wheelchair from their hands. In one study, tetraplegic participants made judgments of whether a doorway was passable with the use of a familiar wheelchair or an unfamiliar wheelchair. As a control, able-bodied participants, who walked for their locomotion, also made the same judgments for walking and wheelchair use. The relative perceptual boundary was determined, which was the ratio of the perceptual boundary between the passable and impassable widths to the actual, minimum passable widths. The results indicated that tetraplegic participants accurately determined passable doorways in both familiar and unfamiliar wheelchairs. This was in contrast to the results in which the control participants

Fig. 9  (A) Locomotor task. A participant was asked to cross a narrow door opening of three widths (1.02, 1.1, and 1.2 times the minimum passable width) without collision. (B) Four forms of locomotion. The length of the horizontal bar and the width of the wheelchair were 63 cm. While holding the bar, a participant grasped the handles of the bar, although the image of the handles is not shown due to technical difficulties. This figure was reproduced with permission from Higuchi et al. (2006)28), ©Springer (2006).
demonstrated less accuracy for the wheelchair condition than for the walking condition. These findings suggest that adaptation to altered body dimensions (i.e., the use of an unfamiliar wheelchair) occurred quickly for those who are familiar with wheelchair use. Given that tetraplegic participants lack somatosensory input from their upper limbs, the findings also suggest that individuals are likely to rely more on visual memory of a passable space than on somatosensory information about the dimensions.

3) Difficulty in adapting to altered action capabilities when using an unfamiliar form of locomotion

Incorporating evidence suggests that an individual’s superior ability to quickly adapt to artificial extensions of the body seems to occur only for well-learned behaviors. We demonstrated that young, able-bodied participants who had never used a wheelchair underestimated the space required for a wheelchair risking potential collisions. These participants determined that apertures would be passable when apertures were greater than 0.94 times the width of the wheelchair. Their underestimation was not completely eliminated even after eight days of practice moving through openings of various widths with a wheelchair. These findings suggest that it would take a long time to adapt to altered action capabilities while using a wheelchair. Because the biomechanical features of locomotion dramatically change from walking to wheelchair use (e.g., upper-limb propulsion, restricted mobility, and dramatic changes in the position of the center of mass and base of support), extensive practice may be required to accurately determine whether safe passage is possible. In fact, the estimation of the space required for wheelchair use was accurate when able-bodied participants were trained to use a wheelchair for six months.

Moreover, an individual’s superior ability to quickly adapt to artificial extensions in a specific context, which is obtained through extensive practice, is not necessarily transferred in a novel context. American football players with extensive practice running through narrow spaces while wearing large shoulder pads exhibited greater efficiency in running through narrow apertures than control athletes. Specifically, football players exhibited smaller magnitudes and later onset times of body rotation than the control athletes. Importantly, however, such differences occurred only when they were running through openings and not while they were walking through them. The results highlight that their excellent ability to quickly adapt to artificial extensions while wearing the shoulder pads is context specific (i.e., speed dependent).

In fact, spatio-temporal patterns of eye movement while approaching and passing through an aperture are completely different for familiar and unfamiliar forms of locomotion (see Fig. 9 for the experimental task during which eye movement was recorded). Fig. 10 (top) demonstrates the average percentages of fixations directed toward each of the four locations (left door, aperture, floor, path, or right door) during walking (i.e., a familiar form of locomotion). For walking, fixations were directed exclusively toward the middle of the opening in the final part of each walking trial (for the last 10% of the normalized walking time). The patterns of fixation remained unchanged when walking while holding a long bar.

However, the spatio-temporal patterns of fixation are dramatically different when using a wheelchair (i.e., an unfamiliar form of locomotion). Fig. 10 (bottom) demonstrates that fixations were directed more frequently toward the door edges throughout their locomotion. At the same time, the duration of each fixation became significantly shorter. By foveating the door edges, the participants were better able to ascertain the door’s position, while short fixation durations allowed the participants to process each door’s location more frequently. The differences in spatio-temporal patterns of fixation while walking or using a wheelchair seem to be similar to those between elite and non-elite athletes in that non-elite participants had shorter fixations and more frequent saccades at critical moments. The clear differences in the spatio-temporal patterns of eye movement indicate that visual information necessary for representing a space in relation to the person-plus-object is different depending on whether the locomotion form is well learned.

4) Improved perception of space for locomotion with altered action capabilities through experience

As explained, it would take a long time to adapt to altered action capabilities when individuals use an unfamiliar form of locomotion. Is there any technique to quickly acquire the ability to perceive the space required for locomotion? Addressing this issue is important, particularly in connection with the fact that some individuals have difficulty with such perception. For example, older adults overestimate their ability to reach an object or step over an obstacle. Overestimation was more evident as their ability to perform the behavior declined. This overestimation could lead them to attempt a behavior that exceeds their action capabilities increasing the risk of tripping or falling.

One might assume that practice performing a given behavior (referred to as direct practice in this study) would lead to rapid improvement in perceiving the space required for that behavior. In fact, some studies have clearly shown immediate effects of direct practice. For example, underestimation of maximum reaching height was significantly reduced after only six attempts to perform a reaching task. In addition, twenty attempts to squeeze through an opening were sufficient for improving perception of the space required for this behavior.

Franchak et al. (2010) proposed that the perception of the space required for locomotion could be improved immediately if direct practice would provide opportunities to detect very fine differences between possible and impossible behaviors. In their study, the participants practiced
However, we recently demonstrated that the immediate effect of direct practice was mediated by the familiarity of the form of locomotion, but not by the resolution of the practice. Participants reported whether apertures of various widths were passable when walking while holding a 69-cm horizontal bar (Exp. 1) or when using a wheelchair (Exp. 2). When practicing passing through apertures, passing through aperture widths that were very close to the action boundary (i.e., the boundary between passable and impassable widths) and that could be adjusted in very fine increments (0.2 cm). Here, we refer to such practice (distributed in small increments in a narrow range around the action boundary) as high-resolution practice. By contrast, Higuchi et al. (2004) failed to demonstrate an effect of direct practice when participants practiced passing through aperture widths that were widely distributed from passable to impassable and were adjusted in 5-cm increments.

However, we recently demonstrated that the immediate effect of direct practice was mediated by the familiarity of the form of locomotion, but not by the resolution of the practice. Participants reported whether apertures of various widths were passable when walking while holding a 69-cm horizontal bar (Exp. 1) or when using a wheelchair (Exp. 2). When practicing passing through apertures, sev-
en different aperture widths, including the minimum passable width (70 cm for both experiments), were presented around the action boundary with 1-cm or 5-cm increments for the high- or low-resolution conditions, respectively. The accuracy of passability perception improved following both high- and low-resolution practice when walking. By contrast, no improvement was observed in any condition when using a wheelchair. In agreement with a number of previous studies in this review, these findings suggest that rapid adaptation is likely to occur when the form of locomotion is familiar.

Importantly, improvements in the perception of space required for a given behavior often transfers to perception of the space required for unpracticed but related behaviors. For example, two minutes of practice operating a wheelchair in a hallway (without passing under barriers) resulted in improvements in perception as to whether the wheelchair could be rolled under a barrier.\(^{49,50}\) In addition, six attempts to perform a vertical reaching task resulted in improved perception of maximum reaching heights for unpracticed reaching tasks (even when the unpracticed means of reaching would increase the person’s reaching ability). Specifically, practice performing an unaided reach improved the perception of maximum reaching height for reaching tasks in which a change of posture (i.e., standing on tiptoes) or use of a hand-held tool increased reaching ability.\(^{47}\) These findings suggest that direct practice performing a behavior is not a necessary condition for rapid improvement of perceiving the space required for that behavior. Rather, the opportunity to explore the task-specific fit between the altered action capabilities and environmental properties is necessary.\(^{51}\)

Concluding remarks: perspectives for current and future studies

In this article, we reviewed psychological and neuroscientific findings regarding tool-body assimilation in the brain. Due to limitations of space, we are only able to present a part of the knowledge accumulated thus far. Moreover, relevant findings continue to appear. For example, Ganesh et al. (2014)\(^{52}\) demonstrated that in tool-use reaching, the human brain operates short-term and long-term processes for tool-body assimilation, based on psychophysical observations and computational models. Itaguchi and Fukuzawa (2014)\(^{53}\) reported effector-independent continuity between hand-use and tool-use in motor control as a function of prior degree of use by comparing reach-to-grasp behaviors with fingers and tools. Regarding application studies, a research group applied the “out of the body” rabbit\(^{54}\) and/or funneling effects to hand-held mobile devices\(^{54}\) and virtual objects.\(^{55}\) Future studies on tool-body assimilation will contribute not only to the elucidation of the behavioral and neuronal functions that characterize humans, but also to the development of our knowledge and technologies to facilitate and enrich our behaviors in daily life.

The present article also focused on locomotion with tools or extracorporeal objects during which individuals involve self-motion. Our daily behaviors are not confined to the desk space, but are expanded to the dynamic space that flows according to whole-body movements in real environments (e.g., commuting, shopping, sporting, and so on). To advance such studies, we encounter technical constraints while investigating the neural mechanisms. For example, during fMRI measurements, participants are fixed in a lying posture and are prohibited from head movement (accordingly, also the trunk). Thus, it is essentially impossible to apply the present most powerful technique to identify the neural correlates of locomotion. However, functional near-infrared spectroscopy (fNIRS) may be available, even though its brain-imaging resolution is lower than fMRI. An fNIRS study\(^{56}\) reported the involvement of the prefrontal and premotor cortices while adapting walking and running speed. In addition, voxel-based morphometry (VBM) using anatomical MRI would also be a potential technique for elucidating the brain mechanisms of human action during locomotion. For example, using VBM, Draganski et al. (2004)\(^{57}\) found training-dependent structural changes in the brains of juggling learners. For VBM, there is no need to measure MRI while the participants are performing the tasks; therefore, it is possible to apply VBM to studies of locomotion. Hi-guchi et al. (2004)\(^{54}\) suggested that it takes a long time to adapt to altered action capabilities when individuals perform unfamiliar forms of locomotion. The long adaptation period may indicate that the adaptation involves structural changes in the brain. We await future technological breakthroughs in brain function measurements. Until then, we can use the best combinations of existing methodologies to expand our research concerning tool-use behavior in daily life.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this article.

Acknowledgments

This study was supported by KAKENHI (2524058 and 26119521) to MM and KAKENHI (24680068 and 25560327) to TH. We thank E. Naito, K. Nakahara, M. Wada, and T. Kochiyama for their helpful comments on this article.

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