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Remodeling of cortical activity for motor control following upper limb loss

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Abstract

Objective—Upper extremity loss presents immediate and lasting challenges for motor control. While sensory and motor representations of the amputated limb undergo plasticity to adjacent areas of the sensorimotor homunculus, it remains unclear whether laterality of motor-related activity is affected by neural reorganization following amputation.

Methods—Using electroencephalography, we evaluated neural activation patterns of formerly right hand dominant persons with upper limb loss (amputees) performing a motor task with their residual right limb, then their sound left limb. We compared activation patterns with left- and right-handed persons performing the same task.

Results—Amputees have involvement of contralateral motor areas when using their sound limb and atypically increased activation of posterior parietal regions when using the affected limb. When using the non-amputated left arm, patterns of activation remains similar to right handed persons using their left arm.

Conclusions—A remodeling of activations from traditionally motor areas into posterior parietal areas occurs for motor planning and execution when using the amputated limb. This may reflect an amputation-specific adaptation of heightened visuospatial feedback for motor control involving the amputated limb.

Significance—These results identify a neuroplastic mechanism for motor control in amputees, which may have great relevance to development of motor rehabilitation paradigms and prosthesis adaptation.

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Conflict of Interest

No authors have any conflicts of interest.

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Keywords

Upper limb amputation; EEG; motor control; neuroplasticity

1. Introduction

Reorganization of neural networks has been evaluated in various clinical populations; however, less is known about neuroplasticity in upper extremity amputees. Upper extremity amputees have shown sensory reorganization (Cohen et al., 1991, Borsook et al., 1998, Chen et al., 1998), which tends to relate strongly to phantom sensations (Karl et al., 2001). While it is commonly thought that motor representations of the missing hand are occupied by the residual limb and lateral motor homunculus (Pascual-Leone et al., 1996), recent evidence suggests that the lateral shift may not always occur (Gagne et al., 2011). While most previous attempts to identify patterns of lateralization utilize transcranial magnetic stimulation (TMS), a criticism is that TMS only measures neural function related to the stimulation site. The use of whole-scalp electroencephalography (EEG) allows us to evaluate hemispheric laterality outcomes in motor areas for planning and execution, and identify novel patterns that may reveal unexpected and meaningful plasticity in amputees.

It remains unclear how hemispheric patterns of limb dominance change as a result of amputation. For persons with partial limb amputation, movements that involve proximal musculature of the residual limb may reduce confounds of type of prostheses when studying neuromotor control. Recent studies have sought to evaluate if proximal versus distal movements affect lateralization of motor planning. In a study on tool use movements that were more proximal (e.g., using a saw) compared to those that are more distal (using scissors) (Maki-Marttunen et al., 2014), findings showed that motor planning of proximal and distal gestures in right handed persons generally utilized left lateralized premotor and inferior parietal lobule areas that are known to be responsible for tool use tasks (Fridman et al., 2004, Wheaton et al., 2005a, Bohlhalter et al., 2009). We can also evaluate similar patterns with use of the left arm, as functional limb dominance may play a role in the hemispheric dominance of action planning (Kelly et al., 2015). In unilateral amputees that reject their prostheses, behavioral adaptation to the resulting one-handedness may present an opportunity for the proximal aspect of the non-dominant arm to display novel neural lateralization patterns.

The goal of this work was to understand if contralateral motor activation for left and right limbs are affected in persons with partial limb loss. We had formerly right hand dominant (right affected) amputees performed a simple, gross proximal arm movement task using the sound (left) and the amputated (right) limbs. By focusing on movement of the proximal upper extremity (i.e., residual limb on the amputated side), we constrained device-specific differences in performing the task. This allowed us to identify whether unique patterns of activation are seen in amputees when using their left ("non-dominant") limb without the confound of functional dexterity of the prosthesis. Neural function while performing motor tasks has been extensively addressed in the neurosciences and can be evaluated using EEG. In particular, beta band (18–22Hz) modulation has been shown to reflect motor planning and

execution, primarily with activation localization over motor areas contralateral to the limb performing the task (Shibasaki et al., 2006). Recent evidence further refines the role of beta modulation, demonstrating that beta oscillations correlate with the excitability of spinal motoneurons (Takemi et al., 2015). Further, it is suggested that decreases in beta power relate to an active disinhibition of brain areas that determine parameters of movement (Brinkman et al., 2014). This evidence for beta band involvement in motor processes reinforces the predictability of laterality measures in left and right-handed persons, where movement tends to yield contralateral sensorimotor cortical activations (Stancak et al., 1997, Solodkin et al., 2001). Previous studies have identified strong outcomes in assessment of motor laterality (Formaggio et al., 2008, Nam et al., 2011) and effector-specific motor planning (Wheaton et al., 2008) when assessing beta band laterality. Beta band activation has been seen in brain areas related to motor preparation, even in tasks involving anticipatory visuospatial attention (Gould et al., 2011). For amputees, it is possible that motor lateralization remains either contralateral, shifted laterally (Pascual-Leone et al., 1996), or involves a completely novel pattern. We will assess this by focusing on power changes (activations) over sensorimotor areas including current source density modelling. As current source density allows us to evaluate the spatial extent of neural activations, we will additionally evaluate current source density of alpha (10–12 Hz) rhythms to evaluate the intrinsic relationship of these rhythms within their cortical generators compared to beta band activity (Pfurtscheller et al., 1999).

As well, we will also identify whether any unique patterns are seen for amputees when using their left (“non-dominant”) limb after chronic (>6 months post injury) amputation. We compared the patterns of amputees to left and right dominant persons performing the same task. This allowed us to compare the motor outcomes in amputees with the lateralization patterns in persons with sound limbs. It was hypothesized that formerly right hand dominant amputees would show patterns of neural activation consistent with maintained contralateral motor activation (similar activations to intact right hand dominant individuals).

2. Methods

2.1 Participants

Twenty-five subjects participated in this study. Before participating in the study, all subjects were consented according to guidelines of the Georgia Institute of Technology Institutional Review Board. Twenty of the subjects were healthy intact individuals. Ten were right hand dominant (6 males, mean age 27.7) and the other ten were left hand dominant (4 males, mean age 23.4) based on the Edinburgh Handedness Inventory (Oldfield, 1971). The remaining five subjects were formerly right hand dominant individuals with a right upper limb amputation (Table 1). Amputees were asked their hand dominance prior to amputation using the Edinburgh Handedness Inventory. All persons were free of phantom sensations or lingering pain from surgeries, and had completed all physical therapy. At the time of visit, all participants had active range of motion of the right shoulder (residual limb) within normal limits in all degrees of motion. Manual muscle testing revealed 5/5 muscle strength in all degrees of motion.

2.2. Setup

All participants (amputees or intact subjects) wore a prosthetic device on their right arm. Persons with intact limbs wore the Fictive Amputee Modeling System (FAMS, (Cusack et al., 2014)), which simulates transradial amputation by constraining the arm in a prosthetic device and eliminating forearm rotation, wrist flexion/extension, and hand movement forcing the user to perform tasks with a split hook terminal device (Cusack et al., 2012, Cusack et al., 2014, Cusack et al., 2016). Amputees wore their own prosthesis on the right arm (Table 1 indicates level of amputation and type of device). Surface electromyography (EMG) was placed on the anterior and posterior deltoid of the right and left arm, and served as a surrogate marker of movement onset. Subjects were fitted with a standard tin 58-channel EEG cap (Electrocap, Eaton, OH) to record neural activity using Synamps 2 (Neuroscan, Charlotte, NC). Electoroculography was also recorded to monitor for eye movements, and was later used for artifact rejection using autoregressive modelling (Cerutti et al., 1988). Data acquisition was performed using a right ear reference at a sampling rate of 1000 Hz and filtered to DC-100 Hz. The left ear was also recorded and used to create (offline) a linked ear reference.

2.3 Tasks

Each participant performed two tasks for approximately 12 minutes each. From a seated position with the arm on an armrest, the first task was to “raise and rotate the left arm”, followed by “raise and rotate the right arm” in separate blocks. Specifically, the participant was to lift the arm from the armrest, elevate their arm (to approximately 90 degrees horizontal flexion) with the elbow fully extended, then rotate at the shoulder. After performing the task one time, participants returned to rest. All intact subjects performed the task while wearing the FAMS device on the right hand and forearm, but with the left arm unrestrained. Amputee participants performed all tasks while wearing their own prosthetic device. Participants were asked to rest for approximately 10 seconds between each movement without counting similar to previous work (Wheaton et al., 2005b), which was monitored by observing the pacing between movements on a visual display of the EMG signal during the study. EMG was also monitored to confirm the absence of mirror movements in all participants, as they were not actuating the terminal device for the motor task (in the case of the body-powered devices, bilateral shoulder flexion opens the terminal device).

2.4 Analysis

The raw EEG data were visually marked to reflect EMG onset using the Edit module of Scan, Neuroscan Software (Charlotte, NC). Data were offline filtered and analyzed using in-house MATLAB (Natick, MA) functions and EEGLAB (Delorme and Makeig, 2004). The EEG data were filtered in upper beta frequency (18–22 Hz) as this frequency is associated with motor activity and execution. Each trial was epoched to begin 4500ms before movement onset and end 2500 ms after movement onset. Epochs were averaged within each subject to obtain a individual averages.

Beta band ERD was used as a metric to measure brain activity relative to a baseline power of 4500 to 4000ms before movement onset. Signal power changes are expressed as magnitude

of power change relative to the baseline ($\text{Power change} = (\text{Power}_{\text{active}} - \text{Power}_{\text{rest}}) / \text{Power}_{\text{rest}}$). Comparisons were made for regions of interest (ROI). Channel groupings, based on the international 10–20 system, were identified for the left and right motor regions, where the left motor (LM) was C1A, C1, C1P and C3 and the right motor (RM) was C2A, C2, C2P and C4. Analysis of variance (ANOVA) analysis was performed using SPSS statistical program (IBM Corporation, Armonk, NY) to evaluate the effects of the factors task (left arm, right arm), region of interest (LM, RM), and subject group (amputee, left hand dominant and right hand dominant) on beta power separately for motor planning (–500 ms – 0 ms relative to EMG onset) and execution (0ms – 500ms relative to EMG onset). Post-hoc Bonferroni corrected t-tests were used to identify significant condition differences, where appropriate ($p < 0.05$).

2.5 EEG current density reconstruction

To confirm localization of scalp projections of ERD in the beta band and compare it to alpha (10–12 Hz) topography, current density reconstruction was performed using CURRY software (version 5, Compumedics Neuroscan, Charlotte, NC). This is a similar methodological approach to prior work in amputees (Chen et al., 2013); however, our focus here is to confirm spatial extent of neural activation between the plotting of ERD head maps and current density. Individual subject anatomical scans were not possible for patient data (due to certain ferrous metallic implants as a result of surgery confirmed in 3/5 patients, 2 patients were unavailable for follow-up scans). This required the use of the template head model in CURRY, which was build using the boundary element method (BEM). EEG electrodes were registered to the scalp surface based on digitized positions in reference to anatomical landmarks (left and right preauricular, and nasion) and aligned to the skin surface. Coefficients of conductivity were selected for the skin (0.25S/m), skull (0.017 S/m), and brain (1.79 S/m) based on previous studies (Yao et al., 2005, Chen et al., 2013). The standardized low resolution brain electromagnetic tomography (sLORETA, (Pascual-Marqui, 2002)) approach was chosen to determine cortical generators of the EEG activity. We focused on the planning activity, from –250ms – –150ms for calculation of current density which reflects a time window of potentially maximal motor planning prior to EMG onset. Current density ($\mu\text{A}/\text{mm}^2$) was normalized based in the highest strength in all conditions, for comparison purposes.

3. Results

3.1 Before movement onset

For motor planning, ANOVA revealed significant main effects of subject group ($F(2, 174) = 12.9$, $p < 0.001$, $\eta^2 = 0.22$) and an interaction effect of regions by task ($F(1, 174) = 6.418$, $p = 0.012$, $\eta^2 = 0.14$) and a 3 way interaction (region x subject group x task, $F(2, 174) = 3.4$, $p = 0.034$, $\eta^2 = 0.17$). No other main or interaction effects survived. Results are seen in Figure 1.

While evaluating the region by task interaction, post-hoc t-tests revealed that LM had greater beta power ERD (herein referred to as “activation”) for the right arm task compared to the left arm task ($p = 0.001$), and the RM had greater activation for the left arm task ($p > 0.001$). Figure 1 reveals an apparent laterality in beta power, where left and right dominant

individuals have greater activation over contralateral motor areas. While amputees show some RM lateralization for the left arm task, it appears that the right arm task shows more activation over parietal areas.

As compared to intact individuals, amputees were found to have significantly greater activation of the contralateral motor areas when using the right arm. Within LM, for the right arm task, amputees had significantly greater activation compared to left ($p=0.003$) and right ($p=0.02$) handed participants. There was no significant difference between left and right-handed intact participants.

During motor planning for the left arm, amputees were found to have contralateral activation more similar to the right-handed participants. Within RM, for the left hand task, amputees showed greater activation than left-handed participants ($p>0.001$). There was no difference between amputees and right-handed persons over RM. As well, left-handed participants showed less activation than right-handed participants ($p=0.005$).

3.2 After movement onset

For motor execution, ANOVA revealed significant main effects of subject group ($F(2,144) = 19.8$, $p < 0.001$, $\eta^2=0.1$) and an interaction effect of regions by task ($F(1, .043) = 7.375$, $p = 0.007$, $\eta^2=0.08$) and a 3-way interaction (region x subject group x task, $F(2,.023)=3.9$, $p = 0.021$, $\eta^2=0.08$). No other main or interaction effects survived. Results are shown in Figure 2.

While evaluating the region by task interaction, post-hoc t-tests revealed that LM had greater activation for the right hand task compared to the left hand task ($p=0.006$), which was not present for RM for the left hand task ($p=0.29$). Amputees were found to have significantly less activation of the contralateral motor areas than right handed persons when using their amputated limb. Within LM, for the right arm task, amputees had significantly less activation compared to right handed participants ($p=0.002$). Within LM for the left arm task, left-handed subjects had less activation compared to right handed subjects ($p=0.02$).

When using their left arm, amputees were found to have patterns of contralateral activation more similar to the right-handed participants. Within RM, amputees were found to have significantly more activation compared to left handed participants ($p=0.009$). There was no difference between amputees and right-handed persons over RM. As well, right-handed participants showed more activation compared to left handed participants ($p>0.001$).

Figure 2 reveals an apparent laterality in beta power, where left and right dominant individuals have more activation over contralateral motor areas. While amputees show RM lateralization for the left hand task, it appears that the right hand task again shows more activation over parietal areas. This was the focus of further post hoc analysis, as described below.

3.3. Parietal involvement

The distributions of the activations (Figures 1 and 2) show that contralateral motor areas are active in task performance. For amputees, and particularly the right arm task, the activations

tend to show a shift into mainly to parietal areas. Due to these findings, we performed a post-hoc comparison of left and right parietal regions of interest (left parietal = TCP1, P5, P3, P1, P3P; right parietal = TCP2, P6, P4, P2, P4P) collapsed across planning and execution. To evaluate the effects of the factors task (left arm, right arm), region of interest (left parietal, right parietal), and subject group (amputee, left hand dominant and right hand dominant) ANOVA was run. ANOVA revealed a significant main effect of subject group ($F(2,0.46)=7.3$, $p=0.01$, $\eta^2=0.2$) and interaction effects of subject group by region ($F(2, 0.19)=3.0$, $p=0.05$, $\eta^2=.22$) and subject by region by task ($F(2, 0.019)=3.07$, $p=0.048$, $\eta^2=.22$).

3.3.1 Amputees versus right handed subjects—Post-hoc testing showed that for the left arm task, amputees had greater activation than right-handed subjects over left ($p=0.01$) and right ($p=0.02$) parietal areas. For the right arm task, amputees again showed greater activation than right-handed persons over left ($p=0.004$) and right ($p=0.006$) parietal areas.

3.3.2 Amputees versus left handed persons—For the left arm task, amputees had significantly greater activation compared to left-handed persons over right ($p=0.001$) but not left ($p=0.5$) parietal areas. It should be noted that the overall right hemisphere activation for amputees using their left arm is higher and more diffuse, but over a spatially congruent area centered over motor regions (Figure 2). For the right arm task, amputees again showed greater activation than left handed persons over left ($p=0.004$) and right ($p=0.005$) parietal areas.

3.4 Current source density mapping

Results from current source density mapping of beta band activity (Figure 3) largely confirm spatial estimation from scalp ERD during the planning phase (Figure 1). In the RHD and LHD groups, contralateral motor activation was seen. Chiefly, when amputees performed the right arm task, bilateral (and mainly right) parieto-occipital areas were involved along with motor areas. This pattern was confirmed consistent across all participants. These patterns were also observed for alpha band activity (Figure 4). Movement of the non-dominant hand tended to show more bilateral motor activation while movement of the dominant limb involved contralateral motor activation. Amputees showed a strong bilateral parieto-occipital involvement along with motor areas.

4. Discussion

To determine if amputation of the dominant arm affects predictable contralateral neural patterns of motor planning and execution, formerly right hand dominant amputees with chronic right upper limb amputation (transradial-transhumeral) were compared to right- and left-dominant intact subjects. This effectively allowed us to evaluate whether neural patterns of motor control on the amputated limb more closely resemble pre-amputation left hemisphere dominance, or potentially shifted laterality driven by neuroplasticity (Pascual-Leone et al., 1996). Overall, the results show that when persons with partial upper limb loss perform actions with the intact part of their amputated limb, contralateral motor areas are engaged, but have an atypical increase of activation at parietal areas in both alpha and beta

rhythms. Further, when using the non-amputated left arm, patterns of activation are more similar to right handed persons using their left arm. These results suggest that overall patterns of hemispheric laterality are maintained in the unaffected limb, but that a remodeling of activations from traditionally motor areas into posterior parietal areas has occurred for both motor planning and execution when using the amputated limb.

In previous work, we focused on identifying neurophysiological outcomes for motor planning in amputees. We proposed that a contributing factor of why amputees experience difficulty in gaining skills with prostheses in customary rehabilitation settings is that they are learning motor skills with a prosthesis from a therapist with intact hands rather than another prosthesis user. When amputees imitate actions of persons with intact limbs that the amputee cannot perform, activation of right parietooccipital areas is seen in motor planning, while imitating other prostheses users shows primarily activation in left parietofrontal areas (Cusack et al., 2012; Cusack et al., 2016). It is thought that the activation of parietooccipital areas is related to increased utilization of neural processing of visuospatial information for motor planning and execution (Buccino et al., 2004) or in attempting to understand the intent of observed actions for which there is no motor template (Van Overwalle et al., 2009). Given the parietal activity seen in the present study in both alpha and beta bands, we suggest that the effects from the prior studies are not purely due to the imitation paradigm, *per se*, but represent a neural adaptation following amputation. Such an adaptation may reflect shifts in neural areas responsible for determining motor parameters (Brinkman et al., 2014) in the amputated limb. While it is possible that alpha changes that occur in this study may reflect visuospatial attention (Babiloni et al., 2006; Hobson, Bishop, 2016), current source density reconstructions in the healthy participants that used the FAMS on their right arm were consistent with sensorimotor activations.

These findings are consistent with prior studies of neuroplasticity following amputation. Recent studies report large-scale changes in neural networks including and beyond sensorimotor areas following amputation (Makin et al., 2015). In a case-study report, it was shown that when observing actions outside of their motor repertoire, amputees recruit areas outside of the expected left parietofrontal system (attributed to the mirror neuron system), additionally areas including the right temporoparietal junction (attributed to the mentalizing system (Van Overwalle et al., 2009, Aziz-Zadeh et al., 2012)). Other studies have also shown motor activation expanded to the parietal areas which correlates with phantom sensations (Bjorkman et al., 2012). While none of our participants reported lingering phantom sensations, in this study activation is best aligned to concerns in motor planning beyond sensation. While the motor task in the present work was a simple raising and rotating the arm, this would naturally involve rotating part of a limb that no longer exists on the amputated side. Prior work has suggested that amputees place a greater emphasis on the visuomotor aspects of a motor task (Blank et al., 2010, Metzger et al., 2010), which is a putative role for the mentalizing system in motor planning (Van Overwalle et al., 2009). This view of neuroplasticity following amputation helps to illustrate the complex neural changes that follow in the cortex, which in the motor system may be influenced by changes in activation of projection areas to sensorimotor cortex (Li et al., 2014, Sammons et al., 2015). Further studies are needed to address how these cortical changes can be influenced by peripheral injury in humans.

Research has shown that use of the amputated limb in daily living correlates to plasticity in the “deprived cortex” (Makin et al., 2013). Thus, if the amputated limb is not used regularly in daily living, this could affect plasticity. The amputees in this study all reported very infrequent, situational use of their devices. One participant (Sub 3) only reported using his iLimb (Touch Bionics, Mansfield, MA) for specific recreational purposes (such as using holding the cue while playing billiards). It is commonplace for amputees to use their residual limb as a stabilizer and use the sound limb (which may be the formerly non-dominant limb) as their “functional” limb (Datta et al., 2004). Many of our participants heavily use their left hands for daily task completion. Despite this, amputees showed patterns and levels of activation with the use of the left hand that was more similar to right handed persons using their left hand. It is difficult to assess “handedness” in persons with limb loss, as many of the methods to identify hand dominance rely on the reporting of behaviors based on preference, which proved to be a difficult concept in our evaluation of the present population. While we did not seek to evaluate control of a skillful or dexterous task that may reveal patterns of functional laterality, our findings generally suggest that proximal control lateralization (Maki-Marttunen et al., 2014) is maintained in chronic amputees. Further studies should identify whether corpus callosum volume in amputees affects hemispheric laterality, as has been identified in persons with sound limbs (Stancak et al., 2002a, Stancak et al., 2002b).

Recent studies that have challenged the traditional role of dominance and non-dominance, where limb specialization (such as dynamic tasks or stabilizing tasks) better reflect the functional roles for the limb and its neural control (Sainburg et al., 2000). This has given rise to the proposal that the inherent control organization of left and right limbs is distinct (Yadav et al., 2011). Given this, it is possible that the maintained neural patterns of the task when performed with the left limb may reflect that while the limb may be functionally different from before amputation to after, the same neural areas are used to control the limb. However, studies of lower extremity amputation demonstrate changes in the cortical processing of sensory stimuli, including ipsilateral sensory cortex (Simoes et al., 2012). This suggests the possibility that sensorimotor control of the sound limb could be affected by lack of feedback from the contralateral limb, as demonstrated in studies of acute deafferentation (Werhahn et al., 2002a, Werhahn et al., 2002b). Understanding the neuroplasticity of the sound limb remains to be evaluated in well-developed cortical mapping studies of motor behavior that may include simultaneous whole-brain imaging. Further, while this preliminary investigation did not involve different task levels, ongoing longitudinal studies are seeking to understand whether stable activation of neural areas is maintained for control strategies of the “non-dominant” sound limb following amputation.

We intentionally focused on a task that involved the use of the residual (proximal) limb as to minimize any differences in prosthetic device types or control. This impacted the number of amputees that could be recruited, as many amputees have limited shoulder strength due to chronic disuse of the affected limb. It is worth evaluating in further studies other tasks for which shoulder strength is a lesser concern. As well, future studies can address whether broader levels of amputation from fingertip to forequarter show similar neural changes. A benefit of using the proximal limb segment is that spatial and temporal errors are more symmetrical for proximal, than distal, tasks (Aune et al., 2016). While we did not evaluate motor performance directly, all participants were compliant with the goals of the task.

Further, we had no precise target for movements, which would have impacted the interpretation of the results as visual targeting has been shown to promote occipital activation (Mizelle et al., 2010). Future studies should evaluate the behavior aspects of laterality in paradigms aimed at behavioral identification of proximal and distal upper limb control.

5. Conclusion

Based on known patterns of lateralization prior to amputation, we expected that for simple motor tasks, formerly right-handed (right affected) amputees would have maintained contralateral dominance for motor control. Findings suggest that while actions with the left arm maintained contralateral activation patterns, right arm actions engaged bilateral posterior parietal areas in motor planning and execution. We propose that this reflects an amputation-specific adaptation of heightened visuospatial feedback for determining motor parameters involving the amputated limb. These results suggest that such an adaptation may be a neuroplastic mechanism for motor control in upper limb loss. This paves the way for future studies aimed at evaluating the role of visuospatial adaptation in behavioral lateralization of motor control, functional rehabilitation, and prosthetic device adaptation.

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Highlights

- The neurophysiology of motor control in persons with upper limb amputation is not well known.
- Amputees show involvement of parieto-occipital areas during movement preparation and execution with the amputated limb.
- This may reflect increased visuospatial feedback for motor control involving the amputated limb.

Figure 1.
Head maps of ERD/ERS seen during motor planning in each group (RHD, right hand dominant; LHD, left hand dominant).

Figure 2.
Head maps of ERD/ERS seen during motor execution in each group (RHD, right hand dominant; LHD, left hand dominant).

Figure 3.
Beta band current source density plotting of motor planning activity in each group.

Figure 4.
Alpha band current source density plotting of motor planning activity in each group.

Table 1
Participant information for the amputee subjects (R, right; TR, transradial; TH, transhumeral).

Subject Number	Age	Sex	Reason for Amputation	Time since Amputation	Years with Device	Former Dominance	Side of Amputation	Level	Device Used
1	38	F	Trauma	4 yrs	2	R	R	TR	Body powered split hook
2	37	M	Trauma	1 yr, 1 mo	1	R	R	TH	Body powered split hook
3	26	M	Trauma	6 yrs, 9 mo	2	R	R	TR	iLimb
4	38	M	Trauma	4 yrs, 10 mo	2	R	R	TR	Body powered split hook
5	42	M	Trauma	6 yrs	2	R	R	TH	Body powered split hook