Neuronal network coherent with hand kinematics during fast repetitive hand movements

Mathieu Bourguignon a,b,*, Veikko Jousmäki a,b, Marc Op de Beeck a, Patrick Van Bogaert a, Serge Goldman a, Xavier De Tiège a

a Laboratoire de Cartographie Fonctionnelle du Cerveau, ULB-Hôpital Erasme, 808 route de Lennik, 1070 Brussels, Belgium
b Brain Research Unit, Low Temperature Laboratory, Aalto University School of Science, Puumiehenkuja 2B, Otaniemi, Espoo, Finland

A R T I C L E   I N F O

Article history:
Received 18 April 2011
Revised 9 August 2011
Accepted 12 September 2011
Available online 22 September 2011

Keywords:
Accelerometer
Hand movements
Kinematics
Magnetoencephalography
Motor cortex

A B S T R A C T

We quantified the coupling between magnetoencephalographic (MEG) cortical signals and the kinematics of fast repetitive voluntary hand movements monitored by a 3-axis accelerometer. Ten healthy right-handed adults performed self-paced flexion-extension movements of right-hand fingers at ~3 Hz with either touching the thumb during flexions (TOUCH) or not (noTOUCH). At the sensor level, we found in all subjects and conditions significant coherence at the movement frequency (F0) and its first harmonic (F1). Coherence values were significantly higher in TOUCH compared to noTOUCH. At the group level, dynamic imaging of coherent sources localized the main source of coherent activity at the left primary motor (M1) hand area, except at F0 TOUCH were the main source was localized at the left primary sensory (S1) hand area. Other coherent brain areas were also identified at right S1-M1 cortices (F0), left dorsolateral prefrontal cortex (F1), left posterior parietal cortex (F0 TOUCH and F1 noTOUCH) and left medial S1-M1 areas (TOUCH).

This study highlights the prominent role of rhythmic neuronal activity phase-locked to movements for the encoding and the integration of key sensori-motor features of limb kinematics. This study also suggests that somatosensory afferences play a key role to sustain a high synchronization level between the neuronal activity in coherent brain areas and hand acceleration. Some coherent brain regions differed between F0 and F1 in both conditions, suggesting that distinct cortical areas are involved in different features of hand kinematics.

© 2011 Elsevier Inc. All rights reserved.

Introduction

Most coordinated voluntary movements require highly synchronized and synergistic neuronal control of antagonistic muscles groups. Unraveling how these movements are generated at the neuronal level represents a major issue in neuroscience and a prerequisite to better understand movement disorders pathophysiology or to improve brain computer interface (BCI) approaches.

Previous human and non-human primate studies have shown that many movement’s kinematics parameters correlate with the neuronal activity in the primary motor (M1) cortex (Ebner et al., 2009). Indeed, single neuron studies performed in non-human primates have shown that neurons in M1 cortex encode various movement parameters such as direction, position, rotation, and movement velocity (Ashe and Georgopoulos, 1994; Caminiti et al., 1990; Carmen et al., 2003; Georgopoulos et al., 1988; Mehring et al., 2003; Moran and Schwartz, 1999; Reina et al., 2001). In addition, other studies have shown that hand movement target and velocity can be successfully inferred from M1 local field potentials (Mehring et al., 2003). At the coarsest recording scale, human electric potentials on the scalp and magnetic fields outside the head demonstrated a robust relationship between time-varying M1 neuronal activity and movement velocity (Kelso et al., 1998; O’Sullivanbhain et al., 1999).

In non-human primates, limb kinematics correlates with neuronal activity recorded at the single-cell or multunit levels in several non-primary brain areas such as premotor cortex, posterior parietal cortex (PPC), and cerebellum (Averbeck et al., 2005; Carmen et al., 2003; Coltz et al., 1999; Moran and Schwartz, 1999; Stark et al., 2007). This finding has been extended in humans by positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) studies, which have shown that the activity in multiple primary and non-primary sensori-motor cortical areas correlates with movement velocity (Lewis et al., 2003; Turner et al., 1998).

High-temporal resolution magnetoencephalographic (MEG) recordings have been used in conjunction with tomographic source reconstruction methods to characterize non-invasively the relationship between neuronal activity throughout the human brain and movement kinematics (Bradberry et al., 2009; Jerbi et al., 2007). These studies used complex visuomotor tasks and identified a large neuronal network involved in the visuomotor control of hand speed. In
Materials and methods

Differences in the brain regions involved at coherent frequencies.

ments, 2) to search for differences in the coherent neuronal network involved in self-initiated fast repetitive hand movement analysis to better describe the CKC phenomenon in two types of general coherent signals in some subjects’ cross-correlogram, could not be distributed coherent neuronal network, as suggested by weaker ipsilateral to coherence (F0 and F1). In addition, the existence of a more allow to characterize the neural network involved in the different coherent activity. Nevertheless, this ECD modeling approach did not cortex contralateral to hand movement as the main source of the time domain using the cross-correlogram pinpointed the hand M1 harmonic (F1, ~6 Hz). Equivalent current dipole (ECD) modeling in movements at the hand movement frequency (F0, ~3 Hz) and its equivalent dipole modeling in the time domain (F0, ~3 Hz) and its first harmonic (F1, ~6 Hz). Equivalent current dipole (ECD) modeling in the time domain using the cross-correlogram pinpointed the hand M1 cortex contralateral to hand movement as the main source of the coherent activity. Nevertheless, this ECD modeling approach did not allow to characterize the neural network involved in the different coherent frequencies (F0 and F1). In addition, the existence of a more distributed coherent neuronal network, as suggested by weaker ipsilateral coherent signals in some subjects’ cross-correlogram, could not be identified with the source reconstruction method used. In this paper, we used the DICS approach in combination with a group-level coherence analysis to better describe the CKC phenomenon in two types of hand movements differing in the amount of tactile synchronous stimulations. This study was specifically designed 1) to characterize the neuronal network involved in self-initiated fast repetitive hand movements, 2) to search for differences in the coherent neuronal network depending on the amount of somatosensory inputs, and 3) to assess differences in the brain regions involved at coherent frequencies.

Materials and methods

Fig. 1 summarizes the corticokinematic coherence method used in this study.

Parts of the data used in this study have been analyzed in a previous study using equivalent current dipole modeling in the time domain (Bourguignon et al., 2011).

Subjects

Ten healthy subjects (range 24–40 yrs; mean age 30.5 yrs; 5 males, 5 females) without any history of neuropsychiatric disease or movement disorders were studied. All subjects were right-handed according to Edinburgh handedness inventory (Oldfield, 1971).

The study was approved by the ULB-Hôpital Erasme Ethics Committee. Subjects participated after informed consent. The measurements were carried out at the ULB-Hôpital Erasme, Brussels, Belgium.

Experimental paradigm

Subjects were asked to make self-paced flexions–extensions of all right-hand fingers at about 3 Hz for 3 min in two conditions differing in the amount of tactile somatosensory inputs. In the touch condition (TOUCH), subjects were asked to touch the thumb with the other fingers during the flexions, leading to a high degree of tactile input from fingers. In the non-touch condition (noTOUCH), they were asked to avoid touching the thumb with the other fingers during the flexions in order to limit as much as possible the level of tactile information. The order of condition was balanced across subjects. In order to minimize effects of visual inputs and eye-movements artifacts, subjects were asked to fixate the gaze at a point in the magnetically shielded room to avoid any gaze contact with the moving hand.

Data acquisition

Neuromagnetic signals were recorded with a whole-scalp-covering neuromagnetometer in a magnetically shielded room...
Head position inside the MEG helmet was continuously monitored using four head tracking coils. The locations of the coils with respect to anatomical fiducials were determined with an electromagnetic tracker (Fastrak, Polhemus, Colchester, VT, USA). The movements of the right index finger were monitored time-locked to MEG signals with a 3-axis Acc (ADXL330 IMEMS Accelerometer, Analog Devices, Inc., Norwood, MA, USA). Time-locked MEG and Acc signals were recorded using a bandpass of 0.1–300 Hz and a sampling rate of 1 kHz. High-resolution 3D-T1 cerebral magnetic resonance images (MRIs) were acquired on a 1.5 Tesla MRI scan (Intera, Philips, The Netherlands).

Data preprocessing

Continuous MEG data were first preprocessed off-line using the signal space separation method to suppress external interferences and to correct for head movements (Taulu et al., 2005). To perform frequency and coherence analyses, continuous data were split into 2048 ms epochs with 1638-ms epoch overlap, leading to a frequency resolution of ~0.5 Hz (Bortel and Sovka, 2007). Such frequency resolution is typically used in coherence analyses (Baker and Baker, 2003; Semmler and Nordstrom, 1998). MEG epochs exceeding 3 pT (magnetometers) or 0.7 pT/cm (gradiometers) were excluded from further analysis to avoid contamination of our data by eye movements, muscle activity, and artifacts in the MEG sensors. These steps led to more than 400 artifact free MEG and Acc epochs for each subject and condition. The acceleration corresponding to each epoch was evaluated at every sample as the Euclidian norm of the three band-passed (1–200 Hz) Acc channels.

Coherence analyses

The coherence is an extension of Pearson correlation coefficient to the frequency domain, which determines the degree of coupling between two signals \( x(t) \) and \( y(t) \), providing a number between 0 (no linear dependency) and 1 (perfect linear dependency) for each frequency (Halliday et al., 1995). Let \( X_f(f) \) and \( Y_f(f) \) be the Fourier transform of the \( k \)th segment of \( x(t) \) and \( y(t) \), by defining

\[
P_{xy,f} = \frac{1}{K} \sum_k X_k(f)Y_k^*(f),
\]

where \( K \) is the number of averaged epochs, the coherence can be written as

\[
\text{Coh}_{xy,f} = \left| \frac{P_{xy,f}(f)}{P_{xx,f}(f)P_{yy,f}(f)} \right|^2.
\]

Considering the linear relationship between acceleration and velocity in the frequency domain, coherence analyses were performed using the acceleration directly available from Acc signals rather than with velocity signals derived from the acceleration by time integration (Bourguignon et al., 2011).

Frequencies of interest

To determine the frequencies used for coherent source analyses, namely the frequencies of interest, coherence spectra were computed using (2) between Acc and MEG signals (i.e. sensor space). Frequencies that showed in all subjects significant coupling between Acc and MEG signals in sensor space were defined as the frequencies of interest. To perform coherent source analyses, the \((N_s + 1 \times N_s + 1)\) cross-spectral density matrix was computed between all possible combinations of MEG and acceleration signals at the frequencies of interest.

Coherent source analyses

Individual MRIs were first segmented using Freesurfer software (Martinos Center for Biomedical Imaging, Massachusetts, USA). Then, the MEG forward model for two orthogonal tangential current dipoles placed on a homogeneous 7 mm grid source space covering the whole brain was computed using MNE suite (Martinos Center for Biomedical Imaging, Massachusetts, USA). Coherence maps at the frequencies of interest were finally produced within the computed source space using the Dynamic Imaging of Coherent Sources (DICS) approach with minimum variance beamformer (Gross et al., 2001). Both planar gradiometers and magnetometers were used for inverse modeling, by using a constant non-adaptive weighting. Magnetometer noise was fixed at 300 fT and gradiometer noise at 50 fT/cm. On average, this weighting gave a slightly higher weight to gradiometer signals as compared to magnetometer signals.

Group level analyses

A 12–parameters affine transformation from individual MRIs to the standard Montreal Neurological Institute (MNI) brain was first computed using the spatial normalization algorithm implemented in Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, London, UK) and then applied to individual MRIs and coherence maps. This procedure generated a normalized coherence map in the MNI space for each subject, condition, and frequency of interest. To produce coherence maps at the group level for each condition and frequency of interest, we computed the generalized \( f \)-mean of individual normalized maps, according to

\[
f(\cdot) = \text{arctanh}(\sqrt{\cdot}),
\]

namely the Fisher z-transform of the square root. This procedure transforms the noise on the coherence into an approximately normally distributed noise (Rosenberg et al., 1989). Therefore, the computed coherence is an unbiased estimation of the mean coherence at the group level. Moreover, this averaging procedure lessens the relative contribution of subjects characterized by high coherence values to the group analysis. Finally, difference of \( f \)-transformed TOUCH–noTOUCH group-level maps (difference maps) was computed.

Statistical analyses

Simulated data were used to assess the threshold for statistical significance of coherence values in single subject’s sensor space and group-level coherence maps. This approach overcomes the multiple comparison issue, which has no straightforward analytical solution when dealing with highly dependent time series.

To assess the statistical significance of our results, for both conditions and frequencies of interest separately, we repeated 10,000 times the procedure of computing subject-level coherence values in the sensor space, group-level coherence maps, and difference maps using real MEG signals and Fourier transform surrogate acceleration signals (Faes et al., 2004). The Fourier transform surrogate imposes power spectrum to remain the same as in the original signal but replaces the phase of Fourier coefficients by random numbers in the range \([-\pi,\pi]\) in the surrogate signals (Faes et al., 2004). Maximal coherence and difference values were then extracted for each simulation to compute the cumulative density function of the maximal coherence and difference values occurring due to stochastic matching between acceleration and MEG sensor or source signals. The coherence or difference thresholds at \( p < 0.05 \) corrected for multiple comparisons were then evaluated as the 0.95 percentile of the corresponding cumulative density function.

Statistical differences between movement frequencies and maximal coherence levels between TOUCH and noTOUCH conditions were assessed using Wilcoxon signed rank test at the sensor level.
Assessment of coherence maps

Local coherence maxima were identified in group-level coherence maps for each condition and frequencies of interest. Only local coherence maxima with values above the statistical threshold were considered. The number of subjects for which normalized coherence maps displayed a local coherence maximum less than 10 mm away from the corresponding group-level local coherence maximum was then determined.

Results

Acceleration and coherence spectra

All subjects performed the tasks with a movement frequency of around 3 Hz. The movement frequency was significantly higher (p = 0.0039) in TOUCH (3.61 ± 0.52 Hz; mean ± sd) than in noTOUCH (2.73 ± 0.66 Hz). In both, TOUCH and noTOUCH, acceleration power spectra and coherence spectra showed peaks at F0 and F1 in all subjects (see Fig. 2). Coherence values at these frequencies were statistically significant for all subjects and conditions (p < 0.05, Table 1). At F0 (varying with subject and condition), maximal coherence values over all sensors were significantly higher in TOUCH than in noTOUCH (p < 0.05). The same tendency was observed at F1 but did not reach significance (p = 0.13). In addition, significant coherence peaks were observed at higher harmonics in some subjects (see Fig. 2). Only F0 and F1 were considered as frequencies of interest for coherent source analyses.

Coherent source analyses

Fig. 3 illustrates the results of coherent source analyses at the group level.

The coherence values for the significant coherent cortical areas at the group level as well as the number of individual subjects in whom those coherent cortical areas were observed are reported in Table 2. At the group level, the maximum coherence was observed at M1 hand area contralateral to hand movements in all frequencies of interest and conditions, except at F0 in TOUCH where S1 hand area was the most coherent brain area. MNI coordinates of the local coherence maximum observed at the left M1 hand area were very close to each other in all conditions and frequencies of interest, with maximum distance of 3.6 mm from the mean coordinate [-40.75 - 17.5 59.5].

Significant local coherence maxima with weaker coherence values were observed across conditions or coherent frequencies in other segregated cortical areas. In the hemisphere contralateral to hand movement, these maxima were located in the dorsolateral prefrontal cortex (DLPFC) at F1 in both conditions, in the medial S1-M1 area at F0 and F1 in TOUCH, and in the PPC at F0 in TOUCH and at F1 in noTOUCH. In the hemisphere ipsilateral to hand movement, local coherence maxima were present only at F0, at S1-M1 area in both conditions.

At F0, difference maps showed that coherence values were significantly higher at all local coherence maxima observed in TOUCH compared with noTOUCH, except at M1 cortex contralateral to hand movement (Fig. 4). At F1, coherence values were significantly higher at M1 cortex contralateral to hand movement in TOUCH compared with noTOUCH. Difference maps also revealed that coherence values were significantly higher in some parieto-frontal regions in TOUCH compared with noTOUCH but no manifest local coherence maximum was identified in these regions in group level coherence maps.

Discussion

Using natural hand movement paradigms and non-invasive MEG recordings, this study shows that rhythmic neuronal activity within an extensive cortical sensori-motor network is coupled with hand acceleration during repetitive self-initiated voluntary hand movements. This study highlights that the main source of the coherent activity at the movement frequency is located in M1 or S1 hand cortical area contralateral to hand movement depending on the amount of tactile somatosensory inputs (TOUCH or noTOUCH). It also demonstrates that coherence values are significantly higher when the movement task is associated with a high level of somatosensory inputs.
In this study, the self-paced nature of the hand movement tasks introduced some degree of inter-subjects and inter-conditions (TOUCH VS noTOUCH) variability in movement frequency. Indeed, movement frequency was significantly higher in TOUCH than in noTOUCH. Interestingly, acceleration power-spectra and coherence-spectra peaked at common frequencies corresponding to hand movement repetition rate and its first harmonic in all subjects. This finding suggests that the CKC frequency varies in accordance with the movement repetition rate. Hence, these data bring further evidences favoring a prominent role for rhythmic neuronal activity phase-locked to movement kinematics for the encoding and the integration of key sensori-motor features of limb movements. By contrast, these data do not support the hypothesis of an intrinsic rhythmic neuronal activity in the coherent brain regions not causally linked to task performance (Jerbi et al., 2007).

Coupling at double the movement frequency has been evidenced in previous studies and its functional relevance is still under debate (Pollok et al., 2004a; Pollok et al., 2005). This study suggests that some coherent brain areas were involved in the processing of voluntary repetitive hand movements depending on which spectral
component of hand acceleration was considered (F0 or F1). Indeed, the DLPFC contralateral to hand movement was only identified at F1 in both conditions and hand S1-M1 areas ipsilateral to hand movement were identified only at F0 in both conditions. This finding suggests that these brain areas might be involved in different aspects of movement kinematics. It could also represent an epiphenomenon related to the fact that the neuronal activity in the DLPFC is not strictly sinusoidal compared to the other coherent brain regions (Pollok et al., 2004a; Pollok et al., 2004b).

The kinematics coherent network

As previously shown by other studies (Bradberry et al., 2009; Jerbi et al., 2007; Pollok et al., 2004a; Pollok et al., 2005), the main cortical source of coherent activity was localized at hand M1 area contralateral to hand movement in both frequencies of interest and conditions, except at F0 in TOUCH where S1 hand area was the most coherent brain area. This finding is consistent with the role of M1 neurons in encoding some hand movement kinematics parameters as revealed by M1 neuronal recordings in non-human primates (Caminiti et al., 1990; Georgopoulos et al., 1988; Moran and Schwartz, 1999) and by whole-scalp MEG recordings in humans (Bradberry et al., 2009; Jerbi et al., 2007). More precisely, non-human primate studies have shown that, in addition to neurons with muscle-like properties, M1 cortex contains neurons involved in the encoding of specific movement kinematics parameters such as hand position, direction, velocity, and acceleration (Kakei et al., 1999; Stark et al., 2007).

At F0 in TOUCH, S1 cortex contralateral to hand movement displayed the highest coherent activity among all brain regions and displayed higher coherence level compared with noTOUCH. This likely reflects the neuronal integration of tactile inputs associated to the contact between the thumb and other fingers at each movement cycle. Interestingly, higher movement frequencies and coherence values at the sensor and source levels were observed during TOUCH compared with noTOUCH. This finding is in agreement with previous studies investigating the corticomuscular coherence (CMC) phenomenon, which have highlighted the important role of sensory afferences in generating the CMC phenomenon (Baker, 2007; Pohja and Salenius, 2003; Serrien et al., 2003; Witham et al., 2010).

In addition, this study revealed the existence of additional weaker local coherence maxima consistently observed across conditions or frequencies of interest. This finding suggests that hand kinematics correlates with neuronal activity in several non-primary brain areas. These brain areas were located in cortical areas involved in motor planning and organization as well as in sensory input integration in the hemisphere contralateral (medial S1-M1 areas, DLPFC, PPC) and ipsilateral (S1-M1 cortices) to hand movement.

Ipsilateral S1-M1 involvement has been previously described in numerous functional MRI and transcranial magnetic stimulation studies during various types of movement paradigms (Cramer et al., 1999; Haaland et al., 2004; Hanakawa et al., 2005; Hutchinson et al., 2002; Kansaku et al., 2005; Kobayashi et al., 2003; Newton et al., 2005; Porro et al., 2000; Verstynen et al., 2005; Ziemen and Hallett, 2001). The functional significance of ipsilateral S1-M1 coherent activity is nevertheless unclear. Indeed, it might reflect an enhanced inter-hemispheric inhibition or a direct involvement of ipsilateral S1-M1 cortical areas in motor control and sensory integration during repetitive hand movements (Kicic et al., 2008; Kobayashi et al., 2003; Stoecckel and Binkofski, 2010). Both hypotheses could account for our results since inhibitory activity as well as ipsilateral motor control and sensory integration should share a common periodicity with hand kinematics. However, as we did not control for the occurrence of left upper limb muscle activity or sensory inputs, we cannot ensure that the coherent activity found in S1-M1 cortices ipsilateral to hand movement was not related to such factors. So, the existence of

![Fig. 4. Difference of f-transformed TOUCH-noTOUCH group-level maps at F0 (Left) and F1 (Right). Maps are thresholded at significance level (P<0.005). Only positive values, corresponding to a higher coherence level in TOUCH as compared to noTOUCH were significant.](image)
ipsilateral S1-M1 coherent activity in the context of self-paced repetitive movements should be investigated in further studies controlling for these aspects.

The DLPCF is thought to integrate multiple instructions to generate an action plan; it is a major control center of goal-directed behaviors (Abe and Hanakawa, 2009). In addition, this brain region is activated during self-initiated tasks, in which decisions are required about the timing of movements (Jenkins et al., 2000; Karch et al., 2009). The DLPCF coherent activity might therefore reflect the involvement of this brain region in the self-initiation of repetitive hand/fingers movements.

Significant coupling was observed at F0 and F1 in TOUCH in medial S1-M1 areas contralateral to hand movement. According to S1 and M1 classical somatotopy, coherent activity in the medial part of S1-M1 area should reflect motor control and somatosensory integration from the proximal upper limb extremity. However, this medial part of the precentral gyrus is involved in some aspects of fingers movements as reported by some studies challenging the classic view of Penfield’s somatotopic organization of S1-M1 area (Geyer et al., 2006; Mulliken et al., 2008; Wolpert et al., 1998). The higher coherence level observed in PPC during TOUCH compared with noTOUCH is in line with this sensori-motor integration hypothesis.

The movement monitoring performed by the PPC is supposed to be involved in continuous movement control and error detection (Mulliken et al., 2008). Its involvement in the CCK phenomenon is in line with previous studies in non-human primates, which showed that during a copy task by joystick manipulation, neuronal ensemble reactivation with previous studies in non-human primates, which showed that the cerebellum is mainly involved in the control of discrete compared to continuous movements (Spencer et al., 2007; Spencer et al., 2003).

**Conclusion**

This study demonstrates that neuronal activity within a large sensorgotor cortical network is coherent with hand kinematics during natural self-paced repetitive hand movements. The main source of the coherent activity at the movement frequency is localized in M1 or S1 hand cortical area contralateral to hand movement depending on the amount of tactile inputs. Coherence values are significantly higher when the movement task is associated with a high level of tactile inputs, highlighting the key role of somatosensory afferences in maintaining a high level of synchronization between hand acceleration and the neuronal activity in coherent brain areas. Other weaker local coherence maxima were observed at cortical areas involved in motor planning and organization as well as in sensory inputs integration in the hemispheres contralateral and ipsilateral to hand movement.

**Acknowledgment**

Mathieu Bourguignon benefits of a research grant from the FRIA (FRS-FNRS, Belgium). Xavier De Tiège is Clinicien-Chercheur Spécialiste at the FRS-FNRS, Belgium. This work was supported by a “Brains Back to Brussels” grant to VJ from the Institut d’Encouragement de la Recherche Scientifique et de l’Innovation de Bruxelles (Brussels, Belgium), the ERC Advanced Grant #232946, the Fonds de la Recherche Scientifique (FRS-FNRS, Belgium, Research Convention 3.461.108) and the Academy of Finland (National Centers of Excellence Program 2006–2011). We thank Helge Kainulainen and Ronny Schreiber at the Brain Research Unit (Aalto University School of Science, Espoo, Finland) for technical support. We thank Pr. Riitta Hari for substantial comments on the manuscript and study.

**References**


Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., Swinnen, S.P., 2003. Internal vs external generation of movements: differential neural pathways involved in voluntary movement (Jueptner et al., 1996). In addition, some data suggest that the cerebellum is mainly involved in the control of discrete compared to continuous movements (Spencer et al., 2007; Spencer et al., 2003).
bimanual coordination performed in the presence or absence of augmented visual feedback. Neuron 11, 764–776.


