



Contents lists available at ScienceDirect

## International Journal of Psychophysiology

journal homepage: [www.elsevier.com/locate/ijpsycho](http://www.elsevier.com/locate/ijpsycho)

## Linking brain, mind and behavior

Scott Makeig<sup>a,b,\*</sup>, Klaus Gramann<sup>a,b</sup>, Tzyy-Ping Jung<sup>a,b</sup>, Terrence J. Sejnowski<sup>b,c,d</sup>, Howard Poizner<sup>b</sup><sup>a</sup> Swartz Center for Computation Neuroscience, University of California San Diego, 9500 Gilman Drive, La Jolla, CA 92093<sup>b</sup> Institute for Neural Computation, University of California San Diego, 9500 Gilman Drive, La Jolla, CA 92093 USA<sup>c</sup> Division of Biological Sciences, University of California San Diego, 9500 Gilman Drive, La Jolla, CA 92093 USA<sup>d</sup> Howard Hughes Medical Institute, Salk Institute for Biological Studies, La Jolla, 92037 USA

## ARTICLE INFO

## Article history:

Received 12 August 2008

Accepted 14 November 2008

Available online 3 May 2009

## Keywords:

EEG

Motion capture

Biomechanics

Mobile

Brain

Imaging

Embodied cognition

## ABSTRACT

Cortical brain areas and dynamics evolved to organize motor behavior in our three-dimensional environment also support more general human cognitive processes. Yet traditional brain imaging paradigms typically allow and record only minimal participant behavior, then reduce the recorded data to single map features of averaged responses. To more fully investigate the complex links between distributed brain dynamics and motivated natural behavior, we propose the development of wearable mobile brain/body imaging (MoBI) systems that continuously capture the wearer's high-density electrical brain and muscle signals, three-dimensional body movements, audiovisual scene and point of regard, plus new data-driven analysis methods to model their interrelationships. The new imaging modality should allow new insights into how spatially distributed brain dynamics support natural human cognition and agency.

© 2009 Elsevier B.V. All rights reserved.

Perhaps the most important challenge for cognitive neuroscience is to observe and understand how distributed brain processes support our natural, active, and every-varying behavior and cognition. Humans are active agents, near continually engaged in actively attempting to fulfill their needs and desires within a complex and ever-changing environment, often in concert and/or competition with other human, animal, and/or mechanical agents. At the same time, concepts tied together under the term “embodied cognition” have become increasingly important in cognitive science and neuroscience. From the viewpoint of embodied cognition, cognitive processes have evolved to optimize the outcome of our body-based behavior within our 3-D environment. Key concepts include:

- Perception and cognition support action.* A primary function of human perception is to assist motor control (Churchland et al., 1994). For example, the dorsal visual pathway directly supports visually guided actions such as grasping (Goodale and Milner, 1992). In monkeys and humans, motor neurons involved in controlling tools are active when pictures of tool use are viewed, even in the absence of overt motor actions or planning (Rizzolatti and Arbib, 1998).
- Cognition is situated and time-pressured.* New information is integrated into our continually evolving present cognitive environment, allowing us to adapt to and predict how events in our

current environment may be influenced by our actions. Action-motivating events typically require timely environment- and situation-appropriate action selection.

- We actively interact with our environment to acquire and maintain situational awareness.* Our typical feeling that we “can see everything” around us rests on the feeling that what we see gives us enough information to know where to actively look for further information, when and if it becomes of interest. To further reduce our brain memory and processing load, we actively manipulate our environment, e.g. by counting on our fingers, writing shopping lists on paper, erecting signposts, referring to maps during navigation, etc.
- Features of our environment become part of our cognitive system.* Our brain's body image extends beyond our physical body (Maravita and Iriki, 2004). For example, a tennis player's racket becomes an integral part of his or her brain/body action system, influencing the environment (the ball) to shape future events (the opponent's return).
- Our imagination and abstract cognition are also body-based.* Even imaginative and abstract cognition, independent of direct physical interaction with the environment, are body-based. For instance, subvocal rehearsal of contents in verbal working memory involves the same brain structures used for speech perception and production (Wilson, 2001) and imagining limb movements produces activity in the same brain areas involved in producing the actual movements (Rizzolatti et al., 2002). We interpret “abstract” linguistic metaphors and even abstract mathematical entities within (“as-if”) virtual environments, such as when we “look forward” to the future, or imagine “the number line” (Núñez, 2006). Our emotional feelings may also involve somatic “as-if” states and events (Damasio et al., 2000).

\* Corresponding author. Tel.: +1 858 458 1927x11; fax: +1 858 458 1847.

E-mail address: [smakeig@ucsd.edu](mailto:smakeig@ucsd.edu) (S. Makeig).URL: <http://sccn.ucsd.edu/~scott> (S. Makeig).

### 1. Functional brain imaging

In the last decade, the new field of cognitive neuroscience has flourished in large part based on the widespread availability of functional brain magnetic resonance imaging (fMRI) systems that make visible some aspects of the intimate relationships between brain metabolism and cognitive processes, following on the earlier success of average event-related potential (ERP) assays of electroencephalographic (EEG) data features linked to cognitive processes. Results of fMRI experiments, in particular, increasingly show that brain areas and activities originally evolved to organize the motor behavior of animals in their three-dimensional (3-D) environments also support human cognition (Rizzolatti et al., 2002). This suggests that joint imaging of human brain activity and motor behavior, heretofore considered infeasible, could be an invaluable resource for understanding the distributed brain dynamic basis of human cognition and behavior. However, the physical constraints of fMRI and other current functional brain imaging modalities severely limit the scope of brain imaging during production of naturally motivated motor behavior, e.g. whole body behavior in normal 3-D environments. Although virtual-reality systems may be used in fMRI or electroencephalographic (EEG) experiments, participants in such experiments neither produce natural behavior nor experience the concomitant proprioceptive and vestibular sensations.

No brain imaging modality besides EEG involves sensors light enough to allow near-complete freedom of movement of the head and body. Nor do other modalities have sufficient time resolution to record brain activity on the time scale of natural motor behavior, making EEG the clear choice for brain imaging of humans performing tasks

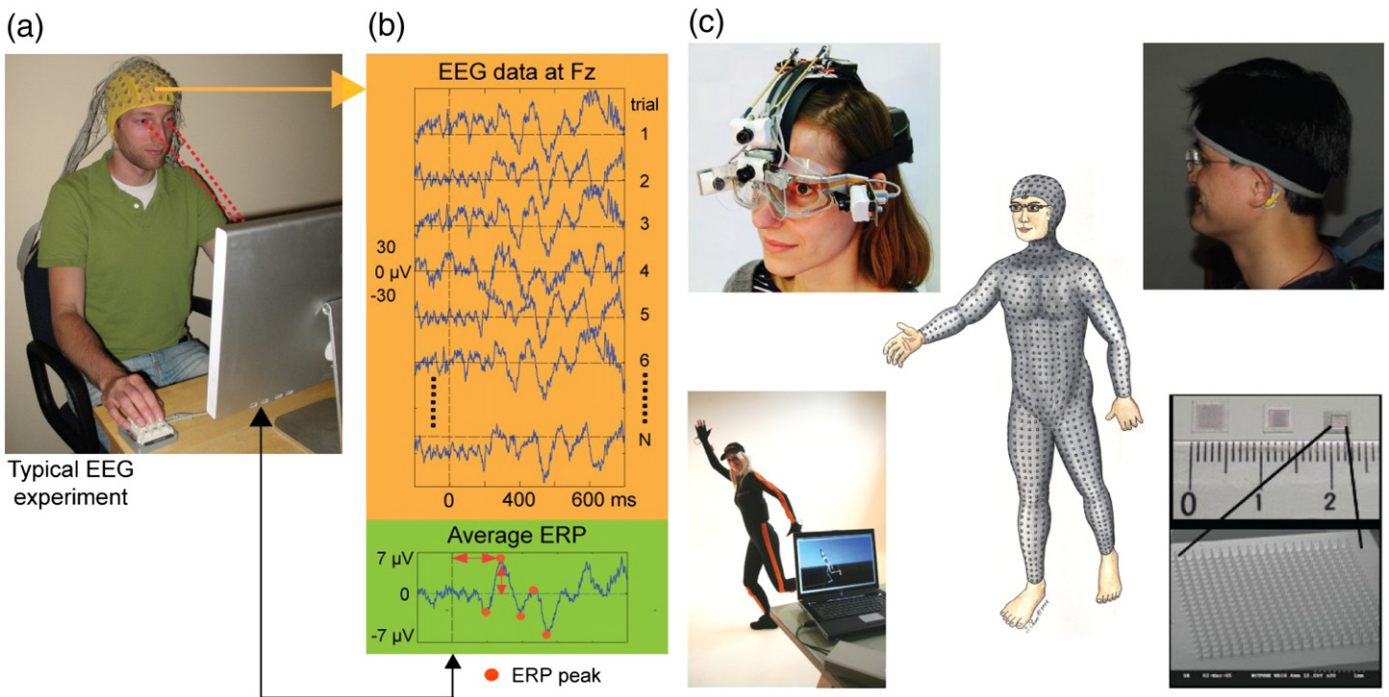
involving natural movements. Unfortunately, traditional EEG experimental paradigms also severely restrict the body, head, and eye movements of participants, largely for fear of introducing non-brain artifacts they produce in traditional EEG system recordings.

### 2. The minimal behavior approach

The tradition of restricting EEG observations to participants performing stereotyped, minimally-active motor responses to sudden onsets of static stimuli continues a long heritage of psychophysical and psychophysiological applications of methods used in classical physics to probe the responses of simple physical systems to external impulses. In traditional EEG experiments, researchers likewise measure only minimal participant behaviors, typically responses to a limited range of suddenly presented stimuli. Because of the perceived difficulty of separating brain EEG data from non-brain artifacts, participants in EEG experiments are asked to sit still, suppressing or minimizing their natural eye and head movements, waiting for stimulus onsets then making small, relatively infrequent finger presses (typically, on one or more “microswitches,” Fig. 1a) to convey their response selections from among a limited range of choices.

### 3. Minimizing data complexity

Simple averaging is then typically used to reduce the collected data to a few average response traces that are then further collapsed into a small table of average response peak amplitudes and latencies



**Fig. 1.** Contrasting typical EEG and proposed MoBl recording methods. (a) A participant in a typical cognitive ERP experiment sits quietly, fixating a cross at screen center, waiting for and then responding to sudden onsets of static visual stimuli with stereotyped, minimized behavioral responses, most often production (“Go”) or withholding (“NoGo”) of minimal finger movements to depress one or more “microswitches.” The only behavioral measures captured are the sequence of times at which the participant delivers (or withholds) button presses. (b) Data epochs from single scalp electrodes time-locked to onsets of (here) some class of visual stimuli presses (orange box) or button presses are then averaged to form a (stimulus-locked (or response-locked) average ERP (green box). The ERP trace is then typically further reduced to a sequence of peak (red disk) amplitude and latency measures. (c) (Center) Artistic concept of a future mobile brain/body imaging (MoBl) system incorporating high-density dry-electrode EEG, microminiaturized eye scene and gaze tracking, and wearable cameraless body motion capture using mm-scale chips embedded in a light skull cap and body stocking. Such a system would dramatically increase the bandwidth of recorded participant behavior and experience. (Upper left) A current prototype scene and gaze-following video recording system (EyeSeeCam, Ludwig-Maximilians-University Munich, Germany) records the scene facing the participant from a central camera, plus a high-resolution record of the subject’s point of regard using a movable (top) camera that follows the participant’s eye movements with a few-ms delay. (Lower left) A current cameraless motion capture suit and portable recording system (Moven, Xsens Technologies, Enschede, Netherlands) records and wirelessly transmits the participant’s body movements without need for external cameras. (Upper right) A prototype four-channel wireless dry electrode EEG system (Lin et al., 2008a,b) incorporating 2 × 2 mm dry electrode chips with 400 ganged contacts (lower right), creating a small textured surface for acquiring signals from non-hairy skin without use of gel.

(Fig. 1b). Finally, researchers look for reliable relationships between these few summary values and, most often, a single behavioral dependent variable, the identity of the button the participant chose to press (or not) in each trial. This approach attempts to reduce the complexity of the recorded EEG dynamics (now easily recorded with a bandwidth of a million or more bits per second) to near the bandwidth of the recorded behavior (typically less than one button selection per second) by averaging across epochs time-locked to sets of events assumed to have similar EEG consequences. Yet, given the complexity and marked moment to moment variability of human EEG dynamics, and the brain's central role in optimizing the outcome of our behavior (on all time scales) in face of ever-changing physical and cognitive circumstances, it is unlikely that this reductive approach to cognitive EEG research can lead to further dramatic advances in understanding how our distributed brain dynamics support our natural behavior and experience.

From a mathematical point of view, the basic problem is that complex functional relationships between two high-dimensional and highly variable signals (EEG and behavior) cannot be well characterized by first reducing each signal to a few average measures and then comparing them. Rather, what is needed is a new and quite different approach incorporating better recording and modeling of relationships between high-density EEG and more natural and higher-fidelity behavioral recordings.

#### 4. A new direction: recording what the brain controls

Clearly, a new experimental approach is required to gain a deeper understanding of the ways in which complex, distributed, and ever-varying neural dynamics support our natural, ever-varying behavior. We propose that this approach should begin with recording as much as possible of the motor behavior and physiological processes, and events that the participant's brain is organizing. Methods for capturing unconstrained multi-joint motions of the head, limbs, and trunk in 3-D space have evolved rapidly over the last 2 decades, engendering a paradigm shift in the field of motor control away from the study of simple movements, such as button presses or single joint motions, to the study of more complexly coordinated, multi-joint naturalistic movements. Positions of dozens of points on the limbs and body can now be captured at high spatial and temporal resolutions during naturalistic movements, and self-contained, "cameraless" motion capture suits are also becoming available (Fig. 1c).

#### 5. Mobile EEG recording

To truly allow high-quality EEG monitoring of naturally-moving subjects, EEG systems must have characteristics not available in current brain imaging systems. To allow dense spatial sampling, the EEG sensors must be small and lightweight, and not require uncomfortable skin preparation. Further, ideally the system should avoid the risk of electrical bridging between nearby contacts by avoiding the use of conductive gel. To minimize weight and susceptibility to system movement artifacts, EEG acquisition and amplification circuits must also be small, lightweight, and battery-powered. To maximize mobility and allow near real-time use of the recorded data or measures derived from it, they may use wireless telemetry. Continuing research into microelectronic biosensors has led to several dry electrode designs (AlizadehTaheri et al., 1996; Gondran et al., 1995; Griss et al., 2001; Lin et al., in press), making truly mobile, wireless EEG systems incorporating dry sensor technology (Fig. 1c, upper right) and small, lightweight, wearable data acquisition circuits now feasible.

#### 6. Audiovisual scene recording

Another behavioral dimension key to our interactions with our environment and other agents is eye movements (Liversedge and

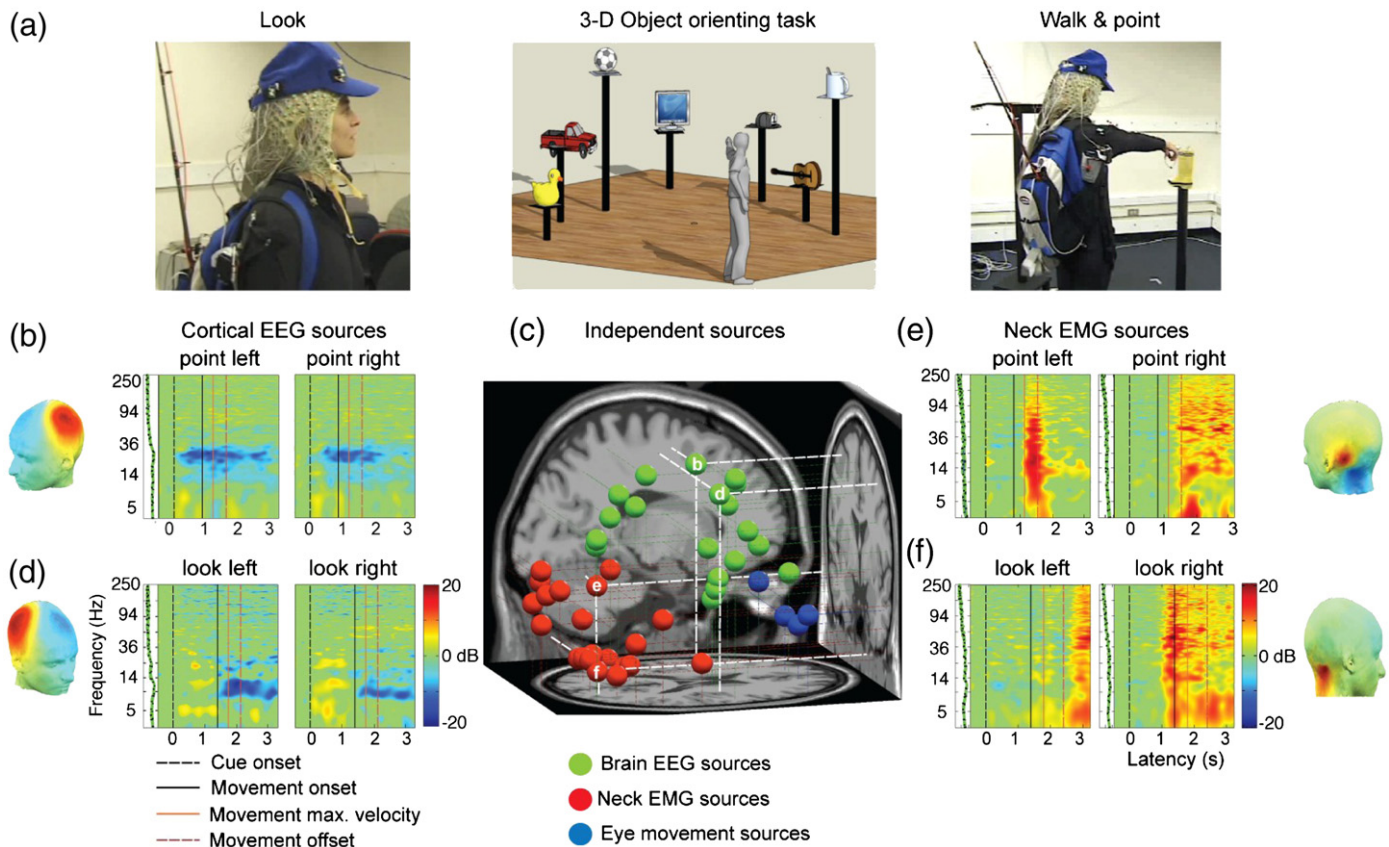
Findlay, 2000). Recording and analysis of eye movements and point of regard of mobile subjects is also challenging. Novel approaches, such as that shown in Fig. 1c (upper left), might in future be miniaturized for wearability, as in the artist conception (center). The brain also supervises the body's autonomic functions, including cardiac activity, respiration, perspiration, etc. (Critchley et al., 2003). It is advisable, therefore, for a more adequate behavioral measurement system to concurrently measure and jointly analyze these functions as well. Recording all this information synchronously poses both a hardware and software engineering challenge. For example, recordings from multiple electrodes placed on and near the neck must sum a large number of distinct head and neck muscle sources. Thus, while current very-high density (256-channel) EEG recordings may adequate for initial development, still higher-density systems using dry electrodes to avoid gel bridging may ultimately prove desirable. A pilot embodiment of the MoBI concept (Fig. 2a) allows recording during an unprecedented although still partially limited range of natural behavior.

#### 7. Mobile EEG analysis

Successful methods for adequate analysis of EEG data in experiments involving a range of participant movements must take into account several factors:

1. *EEG sources.* Scalp EEG signals sum source activities arising within cortical domains whose local field activity becomes partially synchronized, giving rise to far-field potentials that each project, by volume conduction, to nearly all the scalp electrodes, where they are summed with differing relative strengths and polarities (Makeig et al., 2004). Scalp EEG signals also sum a variety of volume-conducted non-brain ("artifact") processes including eye movement, cardiac, and muscle activities, plus line and channel noise, that under favorable circumstances may be separated from the data contributed by brain sources (Jung et al., 2000b).
2. *EEG and movements.* It seems likely the brain may use naturally emergent local field synchronies (cortical EEG sources) to focus its extremely high-dimensional synaptic scale activity onto much lower-dimensional control of motor behavior. If so, then regular relationships between EEG and motor actions may be found in MoBI data, as indeed we and others are already finding. Particularly salient relationships between EEG changes and body movements may occur at movement decision points, particularly when movements are distinctly motivated, for example accompanying quick reactions to unexpected events.
3. *Loci of expected effects.* Many cortical regions are likely interactively involved in supporting motivated motor behavior—not only primary motor areas directly supporting brain motor commands, but also areas supporting motor planning and expectation, perceptual motor and sensorimotor integration, spatial awareness and executive function, including areas directly connected to sub-cortical brain "valuation" systems that support rapid behavioral adjustments to anticipated or potential threats, rewards, and errors.
4. *Correlation versus causation.* Observed relationships between EEG changes and motor actions may not always reflect their direct neural coupling. For example, continual changes in the cortical distribution of alpha band power during inquisitive movements may index concurrent shifts in the distribution of sensory attention (Worden et al., 2000).
5. *EEG artifacts.* A primary challenge to performing EEG brain imaging in mobile circumstances is extracting meaningful event-related brain dynamics from recorded signals that necessarily include significant non-brain artifacts arising from subject eye movements, head and neck electromyographic (EMG) activity, cardiac artifacts, line noise, and other non-brain sources. A signal processing approach developed over the last 2 decades, independent component analysis (ICA) (Bell and Sejnowski, 1995), has proven to be





**Fig. 2.** Pilot mobile brain/body imaging. (a) A pilot 3-D object orienting MoBI experiment. Wearing a lightweight battery-powered 256-channel EEG system (Biosemi, Inc.) and motion capture suit (Phasespace, Inc.) incorporating 30 infrared emitters whose positions are captured at 480 Hz by 12 cameras, the participant turns their head to look toward (left), point to (center), or walk and point to (right) one of several displayed objects as cued by instructions displayed on a task screen (center). Custom (DataRiver) software synchronizes the high-density EEG and full-body motion capture data, stores it, and simultaneously makes it available across a local area network (LAN) for online computation, allowing interactive stimulus control based on current body position or movement and/or EEG measures. The synchronized EEG and behavioral data allow assessment of functional links between brain dynamics and behavior. Independent component analysis (ICA) separates the EEG data into a number of temporally and (often) functionally distinct sources that may be localized, e.g. via their equivalent model dipole(s), as illustrated for one subject in (c). For example, (b) an independent component (IC) source localized to in or near left precentral gyrus (BA 6) exhibits blocking of high-beta band activity following cues to point to objects on the left or right, while another right middle frontal (BA 6) IC source (d) exhibits mean theta- and beta-band increases followed by mu- and beta-band decreases during and after visual orienting to the left or right. (e) An IC source accounting for activity in a left neck muscle produces a burst of broadband EMG activity during left pointing movements, and while maintaining a right pointing stance, while (f) a right neck muscle IC source exhibits an EMG increase during right head turns and during maintenance of left-looking head position.

effective for EEG decomposition into functionally distinct source activities (Makeig and Jung, 1996; Makeig et al., 2002). ICA can be considered a data-driven method that learns a set of spatial filters each of which passes information from a distinct *information source* in the recorded multichannel data (Makeig et al., 2004).

In particular, ICA can be an effective method of identifying and separating several classes of artifacts from the data (Jung et al., 2000a). Under favorable circumstances, ICA decomposition of continuous or discontinuous high-density EEG data allows the separate and concurrent monitoring of dozens of EEG brain and non-brain artifact sources (Fig. 2b, c, d), thus avoiding much of the often severe data reduction integral to traditional analysis methods that reject from analysis EEG data epochs containing movement artifacts. Applied to data from mobile participants, ICA can separate and monitor EMG activity from individual head and neck muscles that, since they do not move appreciably, have spatially fixed patterns of projection to the EEG electrodes (Fig. 2c, e, f). ICA can also isolate into a small component subspace other artifacts whose projections to the recording array are not static but move in spatially stereotyped patterns, for example slow blinks or cardiac artifacts. Spatially labile and non-stereotyped artifacts, however, can quickly spew series of hundreds of unique scalp distributions into the data, each *de facto* independent of the rest of the recorded data and not separable into a

low-dimensional independent component subspace. For example, such artifacts may result if extreme head and scalp movements produce small movements of many of the electrodes on the scalp. Such spatially non-stereotyped artifacts need to be identified and removed from the training data before or during ICA decomposition (Onton et al., 2006).

Finally, electrodes improperly attached to the scalp, most often those placed on labile scalp tissue over face, neck, and scalp muscles, may each contribute independent single-channel noise to some or all of the data, again posing a challenge to artifact separation by standard “complete” ICA methods that train a number of source filters equal to the number of recording channels. While “overcomplete” ICA methods that can learn more filters than this have been developed (Lewicki and Sejnowski, 2000), they require stricter assumptions about the nature of the sources, and may become less robust as signal complexity increases. Therefore, developing methods for identifying and modeling changes in the spatial source distribution of the EEG data is an important goal for ICA research (Lee et al., 1999).

## 8. Brain data preprocessing

Scalp-recorded EEG signals are each mixtures of activity from a variety of brain as well as non-brain sources, and the number of possible brain source domains (e.g., cortical patches) is quite large.

Thus the problem of identifying the unknown EEG source signals and their individual projections to the scalp sensors from the data is a difficult blind source separation and physical inverse problem. Methods and software for imaging the source dynamics of cortical activity from high-density scalp recordings are steadily evolving (Michel et al., 2004). Applied to EEG data, independent component analysis (ICA) algorithms learn spatial filters that linearly separate EEG into a sum of component processes with maximally temporally independent time courses (Makeig et al., 2004; Makeig et al., 1996). Many independent component (IC) source processes project to the scalp with a nearly “dipolar” pattern compatible with a cortical patch source. Spatial equivalent dipole location (in or near brain, else in or near eyes or scalp muscles) can be estimated using an electrical head model, optimally one built from the participant MR head image (Mosher et al., 1999). Open source software is available (Delorme and Makeig, 2004). However, ICA decomposition into separate source activities can be thought of as a signal preprocessing step that enables but does not suffice for joint analysis of the brain EEG and behavioral data. Further, pre-analysis of body motion capture data is also non-trivial.

### 9. Movement data preprocessing

Modern biomechanical data analysis proceeds from recording the changing positions, velocities, and/or accelerations, in external world or body-centered coordinates, of sensors placed on the body surface, to computing movements of each body and limb segment relative to another in a body-centered reference frame, to estimating the time courses of the particular muscular forces that produce those joint movements (Poizner et al., 1995; Soechting and Flanders, 1995). Determining joint movements from motion capture records is a mathematical inverse problem, as a kinematic transformation is needed between trajectories of the recorded body surface positions and those of the underlying joint angles (Soechting and Flanders, 1992). Determining the muscular rotary forces (torques) applied to the limb segments to produce the observed joint/limb trajectories is a further inverse problem requiring a biomechanical model of the body skeleton and musculature (Winter and Eng, 1995), for which open source software is becoming available (Delp et al., 2007).

### 10. Identifying links between behavior and EEG dynamics

To interpret the proposed polymodal mobile brain/body imaging data requires development of adequate methods for modeling relationships between rapidly changing high-dimensional brain source activities and the complexities of natural motor behavior. To discover relationships between high-dimensional synchronously recorded brain and body movement data, they first should each be non-linearly transformed in ways appropriate to the nature and origin of each type of data. Then the structure of the transformed joint data may be explored using data-information based machine learning methods (Baker et al., 2006), and the EEG brain sources imaged using statistical inverse imaging methods (Michel et al., 2004; Wipf et al., 2007). Simple averaging of power spectral changes in independent component time courses unmixed from preliminary MoBI experiments reveal spectral shifts with distinct temporal relationships to particular phases of simple reaching movements (Hammon et al., 2008; Makeig et al., 2007) (Fig. 2b, d). However, new data-driven, multi-factorial analysis methods that identify characteristic time-domain or frequency-domain EEG patterns associated with particular movement and/or task contexts are needed to model the expected richness of the data. Modeling transient coupling between activities of distributed, quasi-independent sources in different brain areas is a further important dimension of data mining and modeling research.

### 11. Open questions

The prospect of EEG-based mobile brain/body imaging (MoBI) raises many methodological, experimental, and theoretical questions:

1. *Recording methods*: How many EEG channels, and what recording montage, sampling rate, and resolution are optimal?
2. *Artifacts*: Within what range of body movements can mobile EEG data be successfully analyzed? How best to identify and deal with movement artifacts in both the EEG and motion capture signals?
3. *Signal processing*: What preprocessing of the EEG and motion-capture signals is optimal for modeling their interrelationships? To what extent is transformation of the body motion capture data to a model of muscle forces and joint angles necessary or desirable?
4. *Psychophysiology*: How can electromyographic (EMG) and other psychophysiological signals (for example, respiratory and electrocardiographic) be incorporated in the analysis?
5. *Audiovisual scene analysis*: How can information about the participant's audiovisual experience and eye gaze history best be incorporated into the analysis?
6. *Context*: How can the moment-by-moment evolution of the experiential and motivational context of participant movements best be observed, represented, and incorporated into the analysis?
7. *Simple movements*: What are the EEG correlates of simple movements such as reaching to touch or grasp objects? How do they depend on the motivation of the action? How do EEG dynamics during walking co-vary with challenges in the terrain? How do they depend on the pace and motivation of the movements? How are they altered in pathologies that affect motor behavior?
8. *Sensory processing*: How are active shifts in attention and body orientation from one object (or agent) to another represented in the EEG? How do EEG dynamics associated with visual processing of presented (2-D) object images (or agents) differ from approaching and viewing the actual (3-D) objects (or agents)?
9. *Learning and memory*: What EEG dynamics are associated with (3-D) spatial learning and with active (3-D) recall?
10. *Motivation*: How do the EEG dynamics associated with externally cued and self-motivated actions differ?
11. *Decision-making*: What EEG dynamics are associated with motor decisions and in-flight motor adjustments, respectively? Again, how does motivation matter?
12. *Abstract cognition*: Do EEG dynamics associated with abstract cognition (for example, counting and use or appreciation of metaphor) resemble dynamics associated with related actions?
13. *Social neuroscience*: What EEG dynamic patterns are associated with orienting to, responding to, and imitating other people versus inert or moving objects? How does this depend on the social context and the intent of the actions?

### 12. Conclusions and future directions

As MoBI technology and analysis methodologies are developed, investigations using a wide range of experimental paradigms will become possible, perhaps beginning with simple motivated actions (such as 3-D orienting, pointing, and grasping as in Fig. 2a) (Hammon et al., 2008), and finally extending to a wide range of tasks and natural behaviors including biomechanical adaptation and learning, navigation, and social interactions. Though many existing experimental designs in all these areas might be fruitfully exploited, the tight coupling between EEG, novelty, and valuation suggest that these factors receive more explicit attention in MoBI experiment designs. The result of combining these sensor development, data analysis, and source imaging technologies should be the development, in coming years, of truly dynamic, higher-definition imaging of distributed EEG brain dynamics supporting natural cognition and behavior.

## Acknowledgments

Invited Keynote Lecture presented at the 14th World Congress of Psychophysiology—the Olympics of the Brain—of the International Organization of Psychophysiology, associated with the United Nations (New York), September 8–13, 2008, St. Petersburg, Russia.

Preparation of this article has been supported by gifts to UCSD from The Swartz Foundation (Old Field, NY), by funding from the National Science Foundation Temporal Dynamics of Learning Center (NSF SBE-0542013), by the National Institutes of Health USA (2R01 NS036449), by funding from the Army Research Laboratory, and by the UCSD Kavli Brain–Mind Institute. The authors acknowledge the technical contributions of Andrey Vankov, Elke Van ERP, and Nima Shamlo Bigdely, and valuable discussions with Daniel Ferris and Rafael Nunez.

## References

- Baker, C.L., Tenenbaum, J.B., Saxe, R.R., 2006. Bayesian models of human action understanding. *Adv. Neur. Info. Process. Sys.*, vol. 18. MIT Press, pp. 99–106.
- Bell, A.J., Sejnowski, T.J., 1995. An information-maximization approach to blind separation and blind deconvolution. *Neural Comput.* 7, 1129–1159.
- Churchland, P.S., Ramachandran, V.S., Sejnowski, T.J., 1994. A critique of pure vision. *Computational neuroscience series. Large-scale neuronal theories of the brain.* MIT Press, pp. 22–60.
- Critchley, H.D., Mathias, C.J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B.K., Cipolotti, L., Shallice, T., Dolan, R.J., 2003. Human cingulate cortex and autonomic control: converging neuroimaging and clinical evidence. *Brain* 126, 2139–2152.
- Damasio, A.R., Grabowski, T.J., Bechara, A., Damasio, H., Ponto, L.L., Parvizi, J., Hichwa, R.D., 2000. Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nat. Neurosci.* 3, 1049–1056.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134, 9–21.
- Delp, S.L., Anderson, F.C., Arnold, A.S., Loan, P., Habib, A., John, C.T., Guendelman, E., Thelen, D.G., 2007. OpenSim: open-source software to create and analyze dynamic simulations of movement. *IEEE Trans. Biomed. Eng.* 54, 1940–1950.
- Gondran, C., Siebert, E., Fabry, P., Novakov, E., Gumery, P.Y., 1995. Non-polarisable dry electrode based on NASICON ceramic. *Med. Biol. Eng. Comput.* 33, 452–457.
- Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25.
- Griss, P., Enoksson, P., Tolvanen-Laakso, H.K., Merilainen, P., Ollmar, S., Stemme, G., 2001. Micromachined electrodes for biopotential measurements. *J. Microelectromech. Syst.* 10, 10–16.
- Hammon, P.S., Makeig, S., Poizner, H., Todorov, E., de Sa, V.R., 2008. Predicting reaching targets from human EEG. *IEEE Signal Process. Mag.* 25, 69–77.
- Jung, T.P., Makeig, S., Humphries, C., Lee, T.W., McKeown, M.J., Iragui, V., Sejnowski, T.J., 2000a. Removing electroencephalographic artifacts by blind source separation. *Psychophysiology* 37, 163–178.
- Jung, T.P., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., Sejnowski, T.J., 2000b. Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clin. Neurophysiol.* 111, 1745–1758.
- Lee, T.W., Girolami, M., Sejnowski, T.J., 1999. Independent component analysis using an extended infomax algorithm for mixed subgaussian and supergaussian sources. *Neural Comput.* 11, 417–441.
- Lewicki, M.S., Sejnowski, T.J., 2000. Learning overcomplete representations. *Neural Comput.* 12, 337–365.
- Lin, C.-T., Ko, L.-W., Chiou, J.-C., Duann, J.-R., Chiu, T.-W., Huang, R.-S., Liang, S.-F., Jung, T.-P., 2008a. Noninvasive neural prostheses using mobile and wireless EEG. *Proc. IEEE* 96, 1167–1193.
- Lin, C.T., Chen, Y.C., Huang, T.Y., Chiu, T.T., Ko, L.W., Liang, S.F., Hsieh, H.Y., Hsu, S.H., Duann, J.R., 2008b. Development of wireless brain computer interface with embedded multitask scheduling and its application on real-time driver's drowsiness detection and warning. *IEEE Trans. Biomed. Eng.* 55, 1582–1591.
- Liversedge, S.P., Findlay, J.M., 2000. Saccadic eye movements and cognition. *Trends Cogn. Sci.* 4, 6–14.
- Makeig, S., Debener, S., Onton, J., Delorme, A., 2004. Mining event-related brain dynamics. *Trends Cogn. Sci.* 8, 204–210.
- Makeig, S., Jung, T.P., 1996. Tonic, phasic, and transient EEG correlates of auditory awareness in drowsiness. *Brain Res.: Cogn. Brain Res.* 4, 15–25.
- Makeig, S., Muller, M.M., Rockstroh, B., 1996. Effects of voluntary movements on early auditory brain responses. *Exp. Brain Res.* 110, 487–492.
- Makeig, S., Onton, J., Sejnowski, T.J., Poizner, H., 2007. Prospects for mobile, high-definition brain imaging: EEG spectral modulations during 3-D reaching. *Human Brain Mapping III, Chicago.*
- Makeig, S., Westerfield, M., Jung, T.P., Enghoff, S., Townsend, J., Courchesne, E., Sejnowski, T.J., 2002. Dynamic brain sources of visual evoked responses. *Science* 295, 690–694.
- Maravita, A., Iriki, A., 2004. Tools for the body (schema). *Trends Cogn. Sci.* 8, 79–86.
- Michel, C.M., Murray, M.M., Lantz, G., Gonzalez, S., Spinelli, L., Grave de Peralta, R., 2004. EEG source imaging. *Clin. Neurophysiol.* 115, 2195–2222.
- Mosher, J.C., Leahy, R.M., Lewis, P.S., 1999. EEG and MEG: forward solutions for inverse methods. *IEEE Trans. Biomed. Eng.* 46, 245–259.
- Núñez, R.E., 2006. Do real numbers really move? Language, thought, and gesture: the embodied foundations of mathematics. In: Hersh, R. (Ed.), *Eighteen unconventional essays on the nature of mathematics.* Springer, New York, pp. 160–181.
- Onton, J., Westerfield, M., Townsend, J., Makeig, S., 2006. Imaging human EEG dynamics using independent component analysis. *Neurosci. Biobehav. Rev.* 30, 808–822.
- Poizner, H., Clark, M.A., Merians, A.S., Macauley, B., Rothi, L.J.G., Heilman, K.M., 1995. Joint coordination deficits in limb apraxia. *Brain* 118, 227–242.
- Rizzolatti, G., Arbib, M.A., 1998. Language within our grasp. *Trends Neurosci.* 21, 188–194.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2002. Motor and cognitive functions of the ventral premotor cortex. *Curr. Opin. Neurobiol.* 12, 149–154.
- Soechting, J.F., Flanders, M., 1992. Moving in 3-dimensional space—frames of reference, vectors, and coordinate systems. *Annu. Rev. Neurosci.* 15, 167–191.
- Soechting, J.F., Flanders, M., 1995. Psychophysical approaches to motor control. *Curr. Opin. Neurobiol.* 5, 742–748.
- Taheri, A., Smith, R.L., Knight, R.T., 1996. An active, microfabricated, scalp electrode array for EEG recording. *Sens. Actuators, A-Phys.* 54, 606–611.
- Wilson, M., 2001. The case for sensorimotor coding in working memory. *Psychon. Bull. Rev.* 8, 44–57.
- Winter, D.A., Eng, P., 1995. Kinetics—our window into the goals and strategies of the central-nervous-system. *Behav. Brain Res.* 67, 111–120.
- Wipf, D., Ramirez, R.R., Palmer, J.A., Makeig, S., Rao, B., 2007. Analysis of empirical Bayesian methods for neuroelectromagnetic source localization. In: Schölkopf, B., Platt, J., Hoffman, T. (Eds.), *Adv. Neur. Info. Process. Sys.* MIT Press.
- Worden, M.S., Foxe, J.J., Wang, N., Simpson, G.V., 2000. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *J. Neurosci.* 20, RC63.