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Cognitive-motor brain–machine interfaces

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Abstract

Brain–machine interfaces (BMIs) open new horizons for the treatment of paralyzed persons, giving hope for the artificial restoration of lost physiological functions. Whereas BMI development has mainly focused on motor rehabilitation, recent studies have suggested that higher cognitive functions can also be deciphered from brain activity, bypassing low level planning and execution functions, and replacing them by computer-controlled effectors. This review describes the new generation of cognitive-motor BMIs, focusing on three BMI types:

1. Speech BMI – reconstructing a person’s speech based on the neuronal activity.
2. Direct object control – controlling object movement without mimicking the limb movement that would yield the desired object movement.
3. Decoding internal processes, such as neuronal representations of sensory information and decision making.

By outlining recent progress in developing these BMI types, we aim to provide a unified view of contemporary research towards the replacement of behavioral outputs of cognitive processes by direct interaction with the brain.

Keywords

Brain–machine interface; Speech; Direct object control; Decision making; Percept decoding; Human neurophysiology

1. Introduction

Brain–machine interfaces (BMIs) are machines that can decode physiological signals from the brain and convert them into actions in a manner that reflects the brain’s intention

(Schwartz, 2004; Birbaumer, 2006; Leuthardt et al., 2006; Moran, 2010). So far, the vast majority of BMI research has focused on the restoration of movement functionality, bypassing paralyzed limbs, and replacing them with external effector such as robotic arms. However, a completely paralyzed person misses other functions as well, like the ability to speak for example, and their restoration can provide tremendous improvement in the patient's ability to communicate with their surroundings.

To undertake these challenges, the realm of brain-machine interfaces may be expanded by using signals recorded from various systems that were traditionally outside the central focus of the BMI field, including higher cognitive processes like working memory, attention, and mental processing networks (Jerbi et al., 2009). These processes, however, incorporate abilities unique to human beings, and therefore research results cannot generally be projected from nonhuman animals to the human, as is common in the motor literature (Georgopoulos et al., 1986; Taylor et al., 2002; Carmena et al., 2003; Paninski et al., 2004; Shoham et al., 2005). Thus, crucial data and insights into aspects of human cognition that may be harnessed for brain-machine interface research and applications relies on the rare opportunities to record in awake humans the intracortical electrical activity of single cells, and of small or large cellular assemblies; previously, such unique clinical opportunities were used to develop a basic-science understanding of neuronal encoding underlying human perception (Mukamel and Fried, 2012). Although these studies are typically performed with able-bodied subjects suffering from intractable epilepsy, movement or affective disorders, there are good reasons to expect that the observed neural encoding will share essential features with volitional activations in paralyzed subjects (Shoham et al., 2001; Kokotilo et al., 2009).

This review focuses on the encoding and decoding of the activity of neuronal ensembles during processes which are on the border between cognitive processes (Andersen et al., 2010; Zander and Kothe, 2011) and motor processes (Hatsopoulos and Donoghue, 2009), and specifically, on the motor expressions of cognitive processes. We note that although functional magnetic resonance imaging (fMRI) can also provide important insights into the neuronal organization of these and related processes, and also has been used for internal process-decoding, it is left mostly outside the scope of this review, primarily because it only provides a very indirect measure of neuronal encoding and is impractical for a real-life BMI.

2. Speech brain-machine interfaces

Speech is perhaps the clearest example of a combination of cognitive and motor processes. Restoring the ability to (artificially) communicate again is a natural way for allowing paralyzed individuals to express their high level thoughts directly to other people, and can greatly improve the quality of life of ALS patients during the late stages of the disease. Indeed, much of BMI work has attempted to address this need indirectly: first by translating motor cortical volitions into binary commands (in the first BMI implanted in the human brain, (Kennedy and Bakay, 1998)) and later on using spelling devices for expressing thoughts in writing, typically controlled using a moving cursor (Birbaumer et al., 1999; Kennedy et al., 2000). Spelling devices can either be controlled noninvasively using either electroencephalography (EEG) (Birbaumer et al., 1999; Guger et al., 2009; Ryan et al.,

2011), or fMRI (Sorger et al., 2012) or invasively, by using electrocorticography (ECoG), e.g., (Krusienski and Shih, 2011) or microelectrodes (Kennedy et al., 2000), see review in (Cecotti, 2011).

A more direct and probably much more natural and intuitive BMI strategy that has only recently been pursued and demonstrated is to directly decode speech and/or speech intentions from speech-related neural activity (for review see: (Brumberg and Guenther, 2010; Brumberg et al., 2010; Pei et al., 2012)). Although the brain areas most commonly associated with speech-production are Broca's and face motor cortex areas, speech production involves a much larger network as described by multiple imaging, lesion and stimulation studies (Mohr, 1976; Ojemann and Mateer, 1979; Ghosh et al., 2008; Sahin et al., 2009; Hickok and Poeppel, 2007; Hickok, 2009; Hickok et al., 2011). The speech production network includes areas in charge of speech comprehension, for example, the bilateral superior temporal gyri (STG), inferior temporal cortex, left angular gyrus, pars orbitalis, and the bilateral superior temporal sulci (Price, 2010). The transition from percepts to actual motor output involves word retrieval (left middle frontal cortex) and articulatory planning (left anterior insula), with initiation and execution of speech controlled by the left putamen, presupplementary motor area (pre-SMA), SMA, and motor cortex (Price, 2010). When no actual motor output is produced, i.e. articulatory imagery, auditory-like responses still occur in auditory cortex, suggesting efference copies still predict the auditory outcome of imagined articulation (Tian & Poeppel, 2010). Imaging studies showed that both the rostral anterior cingulate cortex (Sahin et al., 2009; Paus et al., 1993) and the STG (Buchsbaum et al., 2001; Peeva et al., 2010) also participate in the basic control of speech production, while the medial-frontal orbitofrontal cortex is involved in speech comprehension (Sabri et al., 2008) and reading (Kujala et al., 2007). Anterior cingulate cortex is more active for speech than non-speech vocalization (Chang et al., 2009), and participates in speech motor control in both human (Wise et al., 1999; Sörös et al., 2006) and monkey's vocalizations (Paus, 2001). Speech-related neural activity was characterized most carefully in Broca's area, the region most intimately linked to speech production and its loss in expressive (Broca's) aphasias, and where human studies have been used to characterize the temporal dynamics of speech-related local field potentials (Halgren et al., 1994; Sahin et al., 2009). Much less is known about the encoding of speech production at the single unit level. In a classical study, Ojemann et al. (1988) identified units in STG and adjacent superior margin of the middle temporal gyrus whose activity modulated with overt speech, supporting the area role in the motor aspects of speech, already inferred from the location of lesions producing permanent motor aphasias (Mohr, 1976).

As is usual in the BMI field, ECoG, local field potentials or single unit activity may be employed as signal sources. Although some studies show better performance when employing local field potentials or multiunit activity in comparison with spikes (for example: (Stark and Abeles, 2007)), most studies in the field presume that utilizing the information encoded by populations of single neurons can lead in principle to interfaces with higher information density. The first speech BMI was demonstrated in a paralyzed patient with a neurotrophic microelectrode in his precentral gyrus (Guenther et al., 2009). A Kalman filter-based decoder was trained to predict, from unit firing rates, the intended formant frequencies, which are the spectral peaks of the spectrum envelope amplitude of the

sound (Fant, 1970). These frequencies were then synthesized to provide the subject with audio feedback. The data collected with this patient also served for decoding phonemes from unit firing rates; comparing three classification methods, linear discriminant analysis (LDA), support vector machine (SVM), and flexible discriminant analysis (FDA) – SVM achieved the highest accuracy (21%) for 38 phonemes (i.e., significantly above the chance level of 2.6%) (Brumberg et al., 2011).

In parallel to these early efforts with unit-based speech BMI, other researchers studied the ability to directly decode speech using ECoG – type signals. Kellis et al. (2010) recorded ECoG and micro-ECoG from the surface of face motor cortex and Wernicke's area in an epilepsy patient and classified a set of 10 spoken words on a trial-by-trial basis. Although high accuracy (90%) was achieved on average for all word pairs, it is difficult to compare these results to other studies, because the classified trials were not cross-validated and included only ones with subjectively-selected stereotyped vocal repetitions.

Schalk and colleagues showed that ECoG signals can be used to decode vowels and consonants in spoken or imagined words that could be employed for speech-based BMI systems (Pei et al., 2011). Combining time and frequency domain features, naïve Bayes classifiers obtained similar accuracies for both vowel decoding and consonant decoding tasks: around 40% accuracy for overt and covert speech tasks, significantly above the 25% chance level.

Schalk and colleagues have also demonstrated a cross-modality BMI where ECoG signals associated with different overt and imagined phoneme articulation were utilized for the control of a one-dimensional computer cursor rapidly and accurately. The phonetic content was distinguishable within higher gamma frequency oscillations and enabled users to achieve final target accuracies between 68% and 91% within 15 min. (Leuthardt et al., 2011). They suggested the use of speech-related signals as a cognitive and physiologic substrate for BMI operation, not limited to a speech-producing BMI.

Recently, we used single unit recordings obtained from human subjects during the pronunciation of speech segments, to propose a speech BMI that is based on direct decoding of the phoneme that the user wishes to pronounce (Tankus et al., 2012a) – decoded phonemes can be pre-recorded and played back. The decoder employs neurons recorded mainly from two populations of cells, each of which was found to exhibit a very different type of encoding. In the rostral anterior cingulate and adjacent medial orbitofrontal cortex (rAC/MOF), the encoding is highly specific to individual vowels: units responded sharply during the utterance of only one or two vowels, remaining at the baseline firing rate for other vowels (Fig. 1). In the superior temporal gyrus (STG), on the other hand, non-specific, sinusoidally-modulated tuning takes place: units responded during the utterance of all vowels, but with a gradual change in the firing rate between the different vowel sounds. The tuning is sinusoidal along a dimension representing the highest point of the tongue during articulation, as was determined according to the IPA chart for vowels. This order is natural to the neuronal representation (see (Tankus et al., 2012a, 2012b) for details). Highly accurate prediction of vowel sounds during utterance (93%; chance: 20%) was demonstrated using a new decoder that is based on sparse decomposition for automatic selection of the

task-relevant features to decode from (Tankus et al., 2012b), and which is highly suitable for real-time implementation.

3. Direct object control

The central paradigm of BMI-based restoration of motor functions focuses on reconstruction of volitional hand and arm movements from neuronal activity, mainly in the primary motor cortex (M1) (Carmena et al., 2003; Shoham et al., 2005; Hochberg et al., 2006, 2012; Velliste et al., 2008). In this scheme, when a user plans to manipulate an object, the brain plans and then executes the hand trajectory for performing the action. The BMI decodes this trajectory, and operates an external effector, for example a robotic arm, that will follow this trajectory, to perform the volitional object manipulation.

An alternative approach is to decode the spatial goal toward which the movement is planned (Hwang and Andersen, 2012). Decoding spatial goals could provide this type of BMIs with the ability to rapidly indicate a series of goals, which may benefit speller devices (rapid indication of letters on a letter board) or robotic arms (a smoother transition between a string of movements) (Andersen et al., 2010). The information about movement goals is strongly represented in the premotor (Hatsopoulos et al., 2004) and posterior parietal cortex (Snyder et al., 1997). An example for this type of BMI relies on the spiking activity in the parietal reach region (PRR), which represents the spatial goal of an impending reach when the reach is directed toward or away from a visual object (Hwang and Andersen, 2012). The representation is independent of whether the cue for reaching is direct (showing the target location) or indirect (a symbolic representation of the goal location). The local field potentials (LFPs) in this region were also shown to represent the reach goal when the reach is directed to a visual object. In addition to the goal itself, movement execution onset is signaled by the change in LFP spectrum during transition from planning to execution (Hwang and Andersen, 2009). The goals of eye movements can also be decoded from LFPs in the monkey pre-arcuate gyrus of frontal cortex (Markowitz et al., 2011). Similarly to the aforementioned monkey studies, the human posterior parietal cortex has also been shown to encode prospective plans for upcoming reaching movements while considering targets relevant for action (those to be acquired or avoided) (Lindner et al., 2010). Nevertheless, when considering the application of the PRR-based BMI to human use, the difference in representation between these species (Kagan et al., 2010) will have to be accounted for.

One drawback of this type of BMI is that decoding yields only the final position for the end-effector rather than reconstruction of a complete planned trajectory. Thus, a computer algorithm has to plan an actual trajectory for the end-effector to travel, which may or may not coincide with the trajectory originally intended by the user. As a way of addressing this potential limitation, we recently suggested a novel approach: to reconstruct the trajectory the user wants for the object itself (as opposed to the trajectory of the hand that will manipulate that object). But how can a BMI system know the trajectory the user desires for the object? High-level thoughts of the user, usually based on visual information of the object and internal knowledge of the world, yield desire to manipulate the object. To achieve this, the brain translates the desire into a motor plan for the hands to manipulate the object in a certain way. Somewhere in between these two extremes, visual input and motor plan, lies

the information of what the user wants that will happen to the object (Fig. 2). We therefore suggested to “intercept” the neuronal activity describing the *desired trajectory for the manipulated object*, and have the BMI system move the object along this path (Tankus and Fried, 2012). Thus, the desired object manipulation can potentially be achieved without planning any hand movements. The premise of this technology is based on parahippocampal neurons that encode the desired object kinematics during visuo-motor control over the object (Tankus and Fried, 2012). Thus, the desired object manipulation can potentially be achieved regardless of planning of any hand movements (Fig. 2). The premise of this technology is based on parahippocampal neurons that encode the desired object kinematics during visuo-motor control over the object (Tankus and Fried, 2012). Thus, the desired object manipulation can potentially be achieved regardless of planning of any hand movements (Fig. 2). The premise of this technology is based on parahippocampal neurons that encode the desired object kinematics during visuo-motor control over the object (Tankus and Fried, 2012). Thus, the desired object manipulation can potentially be achieved regardless of planning of any hand movements (Fig. 2). The premise of this technology is based on parahippocampal neurons that encode the desired object kinematics during visuo-motor control over the object. Tankus and Fried (2012) discovered cells in the parahippocampal gyrus which strongly respond to a visuo-motor task, but by far less to the visual aspect of the task by itself, or to its motor-only aspect. These neurons encode kinematic parameters, and thus appear to be part of a control loop connecting visual information processing with generation of actions (hand movements). A sub-population of these neurons was shown to encode the kinematic parameters of object trajectory (or maybe corresponding eye movements), but definitely not hand movement for the implementation of object movement.

The parahippocampal involvement in visuo-motor transformations suggests a physiological basis for the anatomical sub-pathway between the dorsal stream and the medial temporal lobe (Kravitz et al., 2011; Cavada and Goldman-Raiuc, 1989). Thus, the sub-pathway, which connects the angular gyrus and superior occipital gyrus areas (Rushworth et al., 2006) or the lateral intraparietal (LIP) area (Blatt et al., 1990) with the parahippocampal cortex, might be the source of action-guiding visual information to the visuo-motor population we described in the parahippocampal gyrus.

The above sub-population of parahippocampal neurons may be employed for the aforementioned direct object control BMI. This technology is especially attractive for virtual or self-propelled objects (e.g., computer cursors or wheel chairs), where the goal trajectory can be delivered directly to the controlling computer, saving the need for a mediator effector that replaces a nonfunctioning or amputated hand. We note that this approach differs significantly from other cases in the literature where a trajectory was planned while effectively bypassing the manipulator system, like the direct decoding of a desired formant trajectory (Guenther et al., 2009), or 3D hand movement trajectory rather than joint angles (Georgopoulos et al., 1986). Unlike these cases, in the method suggested by Tankus and Fried (2012) the actual movement of a real physical external object is planned, while bypassing planning in terms of the user’s body movement (regardless of coordinate system).

4. Decoding internal processes

4.1. Sensory perception

In addition to studies focusing on decoding brain outputs, or planning processes, a growing number of recent studies decode brain inputs, in various modalities. This trend has three important implications. First, it sheds new light on the information encoded by neural patterns of activity in sensory-perceptual systems. Second, such decoders can serve for BMIs using imagery, in one of two configurations: the user may either directly imagine the information he/she would like to convey (for example, the letter or word he/she wants to write) or alternatively imagine one of a predefined set of conditions whose activity can be classified to select a specific output. An example is a set of mental pictures, each of which is different enough to be distinguished based on the neural activity only, while the output may be a different syllable for each picture (this type of BMI is simpler to implement, because it only requires finding any two brain states whose neural activity is consistently distinguishable from one another, as opposed to using the brain activity representing the two syllables, which may or may not be distinguishable). Third, for the brain's sensory inputs, inference of the detailed parameters and pattern of the neuronal activity, could open an interesting avenue toward direct artificial control of brain inputs by *neuronal stimulation* to induce the neural activity corresponding to (emulating) a certain input, e.g. picture or sound, and thereby activate higher levels of processing of this artificial input, e.g. recognition of the picture or sound.

Reconstruction of auditory stimuli (specifically – their acoustic spectrogram) from neural population responses was demonstrated using a linear spectro-temporal model in the ferret primary auditory cortex (AI) (Mesgarani et al., 2009) and in the songbird auditory midbrain (Ramirez et al., 2011). Recently, Pasley et al. (2012) decoded ECoG activity recorded in the human STG while the patient listened to speech. To decode these signals, they reconstructed slow and intermediate temporal acoustic fluctuations using a linear model based on the auditory spectrogram and fast temporal fluctuations using a nonlinear sound representation based on temporal modulation energy. The decoded speech representations allowed readout and identification of individual words directly from brain activity during single trial sound presentations. Understanding the representation of speech perception may, in the future, allow neural interfaces based on the content of imagined speech. Mesgarani and Chang (2012) reconstructed speech spectrograms based on cortical responses to a mixture of speakers, revealing the salient spectral and temporal features of the attended speaker, as if subjects were listening to that speaker alone. Moreover, a simple classifier trained solely on examples of single speakers decoded both attended words and speaker identity, demonstrating the robustness of decoding in real, multi-speaker environments.

Functional magnetic resonance imaging of a listener's auditory cortex can also be employed for decoding speech content and speaker identity (Formisano et al., 2008). The cortical fingerprints being decoded are spatially distributed and insensitive to acoustic variations of the input so as to permit the brain-based recognition of learned speech from unknown speakers and of learned voices from previously unheard utterances.

In a different type of noninvasive auditory BMI, the subject listens to a steady metronome and has to imagine subjective rhythmization (Vlek et al., 2011). Thus, subjective accents are voluntarily imposed on an auditory metronome. The decoder then classifies single beats from scalp EEG data, distinguishing accented and non-accented beats, or decodes the subjective accents themselves.

Analogous to the aforementioned reconstruction of auditory inputs, several studies have reconstructed spatiotemporal visual inputs from ensembles of neural responses. Stanley et al. (1999) reconstructed natural scenes with recognizable moving objects from neural activity in the cat lateral geniculate nucleus using a linear decoding technique. Pereira (2011) classified higher level concepts based on their fMRI activation in the corresponding brain image. Gallant and colleagues identified natural images from the fMRI signal in visual areas of the human brain and vice versa: predicted the fMRI activation pattern that would be evoked by novel images (Kay et al., 2008; Naselaris et al., 2009). Extending their logic, David and Gallant (2005) were able to predict responses of neurons in the monkey primary visual cortex to natural visual stimuli. These types of models may serve in emulating output to higher-level vision areas, when lower ones are damaged (e.g., predict V1 output to V2 in patients with damaged V1). The goal of visual cortical neuroprosthetics is to interface with the occipital cortex as a means through which a useful sense of vision, even a limited one, could be restored in profoundly blind individuals (see (Normann et al., 2009) for a review). An important underlying question is which distributed stimulation patterns to present; cortical emulation models can potentially be used in this context just as artificial retinas (Mahowald and Mead, 1988; Funatsu et al. (1995); Yagi et al. (1999); Kim et al. (2005); Lorach et al., 2012) could potentially emulate distributed activity patterns for a retinal prosthesis (Reutsky-Gefen et al., 2013). Finally, we note that the recent discovery of medial temporal lobe neurons capable of representing specific images, concepts and recollections (Kreiman et al., 2000; Quiñan-Quiroga et al., 2005; Gelbard-Sagiv et al., 2008) suggests the possibility of explicit decoding of specific thought contents.

4.2. Decision making

The specific outcome of free choices between different plans can be inferred from brain activity, not only after a decision has been made, but even several seconds before it is made, as demonstrated by a modified Libet experiment (Libet et al., 1983) in which subjects freely selected which button to press (left or right) and reported the random letter displayed on the screen at the time they felt the urge to press (Haynes, 2011). Such decisions, which sometimes are followed by a motor activity, can be decoded from neuronal activity, especially in anterior cingulate cortex, medial prefrontal cortex, and ventral striatum, and employed to predict user intention (Hampton and O'Doherty, 2007). To date, BMI systems for locomotion, especially for using wheelchairs or restoration of walking, were proposed under the framework of motor BMI, decoding low level kinematic parameters (Fitzsimmons et al., 2009). Notwithstanding, high-level navigational decisions can be decoded (even prior to the subject's awareness), and may also serve as a method to control navigational BMI systems. For example, the direction to which a driver will turn (left or right) can be predicted with high accuracy from power modulations of gamma band oscillations in intra-

cranial EEG before the conscious decision to turn, as reported by the driver (Perez et al., submitted for publication).

The combination of goal information which represents the probability of earning reward with predicted motor behavior yielded a new BMI framework based on a continuous Perception– Action–Reward Cycle (Mahmoudi and Sanchez, 2011). In this framework, neuronal activity in the rat Nucleus Accumbens was translated into an evaluative feedback for high precision adaptation of the motor decoder, which was based on neuronal activity in M1. The BMI is implemented in an Actor–Critic architecture, where the Actor plays the role of decoding the user’s neural motor commands, and the Critic translates the neural feedback into a temporal-difference error (evaluative feedback) for adaptation of the Actor.

5. Conclusions

Our review focused on the transition from high level cognitive processes to their motor expression and on internal processes for sensory perception and decision making. Recent studies suggest that it is possible to decode the neural activity related to these cognitive-motor processes, and predict the behavior or internal representation. While still in early stages, it is now becoming possible to predict with rapidly improving accuracies not only motor behaviors, but also speech segments, the desired object kinematics (without reconstructing hand movements), goals of eye movements, the internal representations of auditory and visual percepts, and decisions being made by the subject. As an increasing number of higher physiological functions become restorable by brain–machine interfaces, it seems that in the long run, fully locked-in patients (Posner et al., 2007) may be able to experience multimodal physiological rehabilitation not limited to a simple motor output. Much of the progress in this field relies on the development of a better understanding of the encoding of cognitive-motor processes and transformations by neuronal populations or related neural signals, and the complementary development of more powerful decoding schemes.

Conceptually, these technologies may, in the future, move beyond the rehabilitation of paralyzed patients. For example, noninvasive or minimally-invasive technologies may be employed for direct “spoken” communication in environments where silence needs to be maintained, in either general-use or military applications. Philosophically, the possible future ability to observe the brain’s internal cognitive processes or dissociate one’s interaction with the outside world from one’s own body, having his cognition directly interact with the environment in a complex manner, raises new ethical questions which need to be answered as technology develops (Clausen, 2008; Fins et al., 2011), as well as other philosophical questions about the concept of the self, because BMI technology could in principle produce a sense of presence as high as the levels experienced in the physical world, to an extent even larger than virtual reality does (Riva et al., 2004).

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Abbreviations

BMI	brain–machine interface
M1	primary motor cortex
PRR	parietal reach region
rAC/MOF	rostral anterior cingulate and adjacent medial orbitofrontal cortex
STG	superior temporal gyrus
V1, V2, V3, V3A, V3B, V4	areas of the visual cortex
EEG	electroencephalography
ECoG	electrocorticography
fMRI	functional magnetic resonance imaging
LFP	local field potential
FDA	flexible discriminant analysis
LDA	linear discriminant analysis
SVM	support vector machine

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Fig. 1. Speech encoding by single units. (A) A unit in rAC/MOF sharply-tuned to the utterance of “a”. The firing of the unit (vertical red lines) and the sound waveform (blue graphs) during the utterance of two sequences of phonemes, “a” and “e”, are plotted. Three events are zoomed: two utterances of “a”, which demonstrate increased firing rate, and one utterance of “e”, where firing remained at the baseline level. The firing rate of this unit increased from a baseline of about 6 spikes/s to about 97 spikes/s for utterances of “a”, but maintained the baseline level for the rest of the vowels recorded (“e”, “i”, “o”, and “u”), (B) brain areas where speech encoding neurons were found: rAC/ MOF and STG, and (C) example of three units in rAC/MOF, each showing a highly specific response selectivity to individual vowels. D. Four units in STG exhibiting sinusoidally modulated response tuning.

Fig. 2.

(A) Information flow for BMI for direct object control. In non-paralyzed persons, the brain receives visual information of the controlled object, which, combined with internal knowledge of the world, translates into higher-level thoughts. These high-level thoughts lead to the desire of the brain that the digger will move in a certain way, which is then translated into a concrete motor plan for the hand muscles to move the mechanical control levers. The plan describes the required muscle activation for obtaining the desired digger movement. A direct object control BMI is designed to “intercept” the neural representation of the desired

object kinematics, and translate it into direct commands for controlling the electrical controller of the digger (red arrows). It thus bypasses the motor plan, the end effector (hand), and the mechanical levers. No hand movement is reconstructed – control is achieved in object space and (Photo by Ryan Somma of ideonexus.com.) (B) an example of a visumotor neuron in the right parahippocampal gyrus. The firing rate (red) of this neuron is highly correlated with the speed profile (blue) during the visuomotor task but to a much lower extent during visual-only or motor-only tasks.