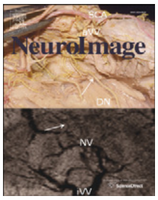
NeuroImage 59 (2012) 14–24

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Review

Decoding intention: A neuroergonomic perspective

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ARTICLE INFO

Article history:
Received 19 March 2011
Revised 20 May 2011
Accepted 21 May 2011
Available online 30 May 2011

Keywords:
Action understanding
Action semantics
N400
Mu-rhythm
Body motion

ABSTRACT

Decoding the intentions of other people based on non-linguistic cues such as their body movement is a major requirement of many jobs. Whether it is maintaining security at an airport or negotiating with locals in a foreign country, there is a need to maximize the effectiveness of training or real-time performance in this decoding process. This review considers the potential utility of neuroergonomic solutions, and in particular, of electroencephalographic (EEG) methods for augmenting action understanding. Focus is given to body movements and hand–object interactions, where there is a rapid growth in relevant science. The interpretation of EEG-based signals is reinforced by a consideration of functional magnetic resonance imaging experiments demonstrating underlying brain mechanisms that support goal oriented action. While no EEG method is currently implemented as a practical application for enhancing the understanding of unspoken intentions, there are a number of promising approaches that merit further development.

Contents

Introduction

Neuroergonomics integrates knowledge of brain function with measurements of behavior that are acquired "at work" to develop methods that can enhance performance (Parasuraman and Wilson, 2008). This paper reviews recent experiments where the work at hand involves observing motor behavior performed by other people and using this information in forming judgments, decisions, or actions. Body movement comes in many forms, from nuanced changes of posture to the grasping or manipulation of a tool. This review considers how some of these complex and varied behaviors are decoded or interpreted in the brain, with a long range goal of improving work environments requiring judgments about another person's actions or intention. These work environments are plentiful and increasing. The worker is faced with maintaining high

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1053-8119/$ – see front matter
doi:10.1016/j.neuroimage.2011.05.064

classification accuracy in the face of severe demands such as high throughput, stress, and potential physical threat. Almost every security force in the world is faced with making fast and accurate decisions about the intentions of human agents. Familiar examples include border security (passport control), standoff procedures (checkpoints), high throughput screening (TSA) and video surveillance (security cameras). In all these examples, impending actions are uncertain, and situated in rich and changing contexts and shaped by an enormous range of cultural influences.

This review builds mainly on experiments in action understanding that involve objects and their use in the environment. Communicative gestures and facial expressions are not addressed here. Instead we focus on a narrow, yet data rich approach that is motivating a number of functional anatomic principles that may eventually generalize to other types of action understanding including movements of the whole body situated in dynamic contexts. In a complementary companion paper of this special issue, Thompson and Parasuraman (this issue) show how attention has a major influence on the decoding of body motion. Our review begins with an overview of imaging studies that record brain activity while people are engaged in the observation of another's action. Admittedly positron emission tomography (PET) and MRI scanners are not readily deployable from a neuroergonomic perspective. Nevertheless, data from functional imaging is essential for building a comprehensive assessment of the neural systems that support action understanding. This understanding of functional anatomy can then be used for improving the interpretation of less spatially determinate but temporally fast and portable methods such as EEG. A key insight from these imaging experiments is that action decoding throughout the brain is both modular and hierarchical in nature. The functional organization of higher order visual and motor systems serving to decode intention therefore echoes that of the earlier visual system carrying out the initial sensory sweep. The review continues with a consideration of action semantics in light of evidence that the particular objects with which an agent interacts and the surrounding context influence action understanding. The emphasis then shifts to electrophysiological methods that could provide potential signatures of action understanding and that hold promise for in-field operability. The current and future utility of these methods for assessing action decoding in real time and using this information to enhance performance in applied settings are compared.

Modularity of action observation

When people observe action performed by another person there is engagement of a widespread, bilateral network of cortical brain regions as measured by either PET imaging of cerebral blood flow or functional magnetic resonance imaging (fMRI) of blood oxygen level-dependent (BOLD) signals (Buccino et al., 2001; Decety et al., 1997; Grafton et al., 1996; Grezes and Decety, 2001; Johnson-Frey et al., 2003; Rizzolatti et al., 1996; Saygin et al., 2004b; Zentgraf et al., 2005). This network is referred to here as the action observation network (AON) and is shown in Fig. 1. At a minimum, it encompasses the bilateral posterior superior temporal sulcus (STS) and adjacent middle and superior temporal gyri (MTG, STG). These span a functional area commonly referred to as the extrastriate body area (EBA) sensitive to viewing of body motion. It also includes inferior parietal lobule (IPL), inferior frontal gyrus (IFG), dorsal premotor cortex (PMd), and ventral premotor cortex (PMv). Depending on experimental details there can also be recruitment of visual processing areas for objects including lateral occipital cortex (LOC). Almost any perceptual stimuli that include body motion will recruit many components of this network (Saygin et al., 2004b). It is striking that the network composition spans cortex demarcated traditionally as specialized for either visual or motor processes. In action understanding, there is no such demarcation between vision and motor systems. The action observation network is highly modular and supports many subtasks that span perceptual, cognitive, and motor domains, including the detection of animacy (Blakemore et al., 2003; Schultz et al., 2005), the identification of biologically meaningful motion (Thompson et al., 2005; Urgesi et al., 2007; Urgesi et al., 2006), identification of body postures such as viewing images of yoga poses (Cross et al., 2010), identification of the agent performing the action (Carter et al., 2011; Liew et al., in press), identification of objects (Kourtzi and Kanwisher, 2000; Xu, 2009), object identification (Beauchamp et al., 2004), assessment of motion smoothness (Miura et al., 2010), retrieval of functional knowledge linked to objects (Weisberg et al., 2007), prediction of temporal and spatially structured stimuli (Schubotz and von Cramon, 2004) and the detection of prosodic or emotional content linked to an object or action (Wyk et al., 2009). The action observation network is also sensitive to physical experience (Wright et al., 2010). Many studies show greater activity in the AON when the observer watches actions that are physically familiar to the observer (Calvo-Merino et al., 2005; Calvo-Merino et al., 2006; Cross et al., 2006). The challenge for neuroergonomics is to understand how these modules supporting a range of subtasks interact to integrate action understanding with specific task challenges and to find associated physiological signatures that can serve as markers for use in maximizing performance in real-world settings.

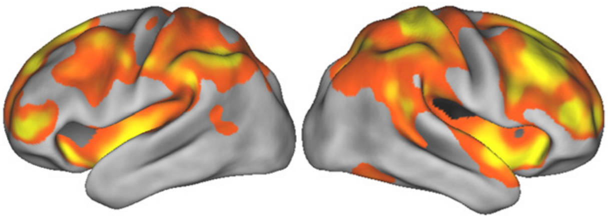

Fig. 1. The action observation network as defined by fMRI. Cortical regions demonstrating significant recruitment during the observation of a hand reaching and grasping a lever, pushing or pulling the lever, and observing the outcome (a lamp turning on or off). In this case, the actions were observed in a virtual environment. Nevertheless, the pattern of activity in the AON is similar to what is observed in movies and real, directly observed actions. When actions include information about the outcome or intention of agent, there is increased recruitment bilaterally in both frontal, parietal and posterior temporal cortex, as shown here. Data taken from a sample of 24 subjects, statistical threshold $p < 0.05$ FDR corrected.

Hierarchical decoding of goals and means

It is safe to claim that most people cannot help but interpret observed actions in terms of goals or outcomes. Actions are conceived in relation to the intended end state, even if this end state is not attained in every particular instance (Csibra and Gergely, 2007). This inclination toward goals and the conceptual parsing of a visual stream into a parts–whole organization emerges at a very early stage of development and can even be detected in young infants (Baldwin et al., 2001; Csibra, 2003; Southgate et al., 2009) or in children using imitation studies (Bekkering et al., 2000). Given this strong conceptual organization around action goals, it is reasonable to ask if the modular organization of the AON reflects an analogous functional parsing of brain activity for constructing action understanding. One possibility is that the integration of brain activity across the modules of the AON is not shaped by a particular organizational structure. Shared information from multiple modules would be integrated ad hoc or through a non-sequential feature integration procedure until a representation of an intention existed. Alternatively, this integration may be a structured process in which modular activity in the AON reflects a functional hierarchy, with some subtasks embedded within higher order processes. For example, the different "means" of an action might be decoded before the "ends" of the action can be determined, and these two steps would rely on different cortex. This structured approach has parallels in computational models that use hierarchy to model the organization of goal oriented behavior. They generally assume that actions have a part–whole organization that is reflected in the hierarchical organization of the constituent modular neural representations (Botvinick, 2008; Cooper and Shallice, 2006). For example, Fig. 2 illustrates the nested, hierarchical organization of the task of parking a car. This relatively straightforward task consists of multiple levels of means and goals, which may be distinguishable not only conceptually, but also neurally in the representation of action. Would a similar organization be used when watching someone else make coffee? This analysis first requires the parsing of a visual stream into subparts based on learned statistical regularities. This parsing allows for segmentation of an action into logical or whole sections of behavior, analogous to the segmentation occurring in language (Baldwin et al., 2008).

It has been challenging in functional imaging experiments to determine if measured brain activity is consistent with this parts–whole model. This requires successive ordering or levels of functional anatomy that directly map to a part–whole structure. This needs to be distinguished from functional differences in non-hierarchical processes such as complexity, task maintenance and scheduling. In other words, demonstrating that different parts of the brain are activated as a function of task complexity or abstraction by itself is insufficient toward establishing that the underlying functional anatomy is hierarchical (Badre and D'Esposito, 2007). It is also necessary to demonstrate that there is a nesting of part–whole processes, with higher levels dependent on lower levels. This nesting cannot be demonstrated with conventional cognitive subtraction paradigms. However, nesting can be shown with the fMRI technique of repetition suppression (RS). RS has been used extensively in studies of visual processing (Grill-Spector et al., 2006; Kourtzi and Kanwisher, 2000), where it is also referred to as “fMRI-adaptation”. It is based on the trial-by-trial reduction of a physiologic response to repeated stimuli. Suppression occurs when two successive stimuli are represented in the same neural population, and release from suppression occurs when two successive stimuli are represented in different populations. RS assumes that the same population will respond differently when the same stimulus feature is repeated. This is demonstrated in Fig. 3, for an action that varies along two dimensions, means and outcomes. The neural mechanism(s) of this change in the BOLD-fMRI response are not known. It could be due to a reduction of neuronal firing, a decrease in firing duration, or a sharpening of neuronal tuning curves (Grill-Spector et al., 2006; Krekelberg et al., 2006). Irrespective of these different mechanisms for RS, at the population level the effects on the BOLD-fMRI signal are all the same. Most importantly, RS can reveal processing specificity at a single level within a potential representational hierarchy for a given class of stimuli. This has a particular benefit for processes that cannot be broken apart with cognitive subtraction. For example, in watching someone grasp a coffee cup, it is not possible to isolate the hand grasp from the object using standard methods. However, with RS, it is possible to find brain areas sensitive to the grasp specification and separately, what is being grasped. This feature of RS provides a powerful tool for mapping modular brain activity to conceptual representational structures, thereby allowing the assessment of nested, hierarchical organization in complex brain systems such as the AON, as shown in Fig. 3.

In a comprehensive series of RS experiments on action understanding, Hamilton employed a library of videos of simple hand–object interactions that varied across a range of action features. For example, in each video the agent reached and grasped objects that varied in identity and/or location. Comparing trials in which either one of these features was novel to those in which that feature was repeated, she demonstrated that the observer's brain had some regions sensitive to *where* an object was located (hand transport) and other regions sensitive to *what* was being grasped (Hamilton and Grafton, 2006). In this work, the object itself was construed as the "goal" and goal related activity was localized to left anterior intraparietal sulcus (aIPS). Studies involving action execution also support the notion that aIPS represents a motor goal centered on the object. fMRI studies show that aIPS plays a central role in representing hand–object

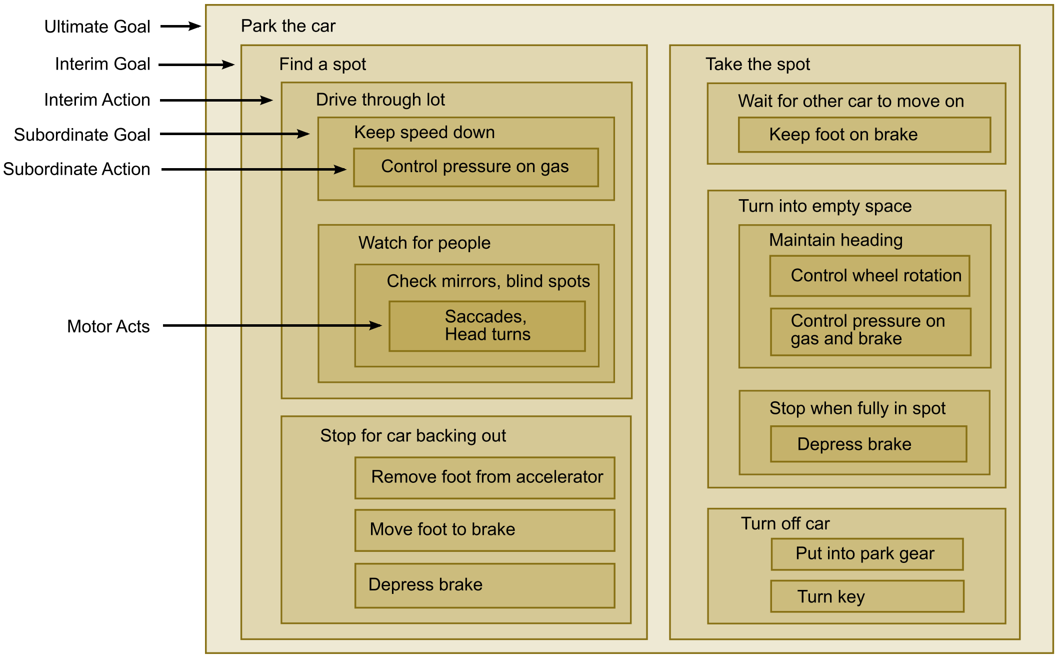

Fig. 2. Hierarchical organization of the task of parking a car. The ultimate goal of parking a car subsumes several levels of means and goals. Completion of the ultimate goal requires completion of interim goals by way of specific actions. The parts and whole structure of conceptualizing complex goals is apparent, as is the nesting of subordinate actions within more complex actions. Imaging studies suggest that action understanding in the brain is sensitive to this nested hierarchical structure. Importantly, what is coded in the brain as an outcome and what is coded as a means to that outcome may vary depending on what level of this conceptual structure is being represented. The required level of representation depends on the context, the task at hand, and the information available to the observer at the time of testing.

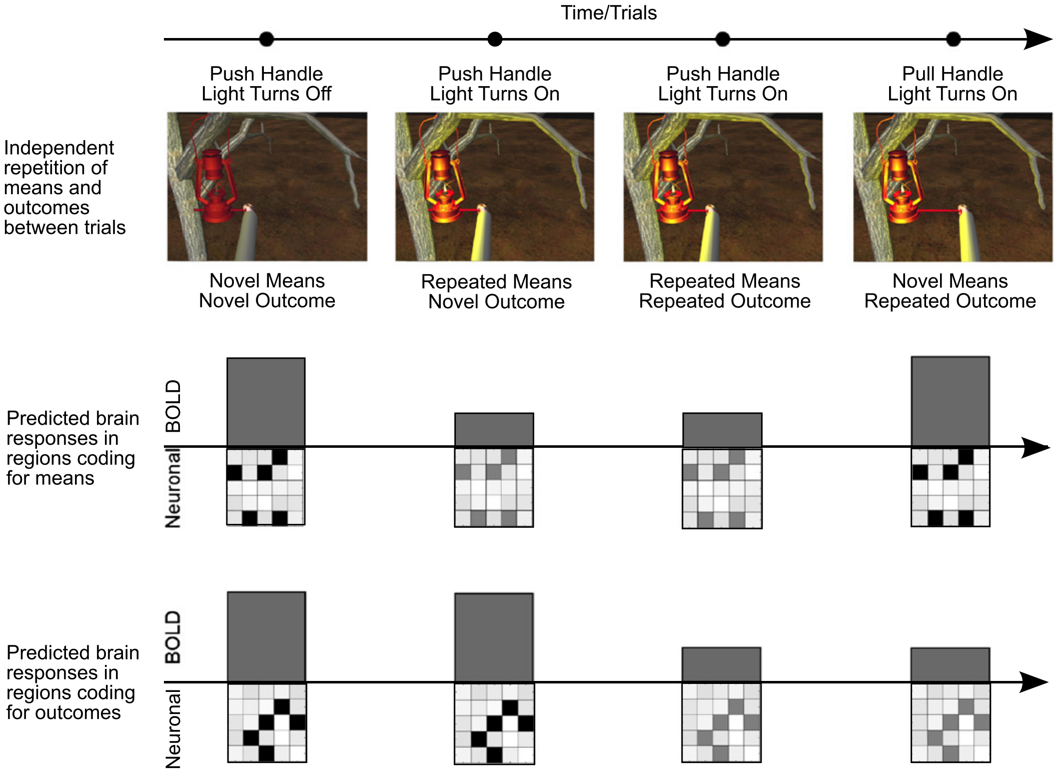

Fig. 3. Repetition suppression used to isolate two levels of action representation. The upper row illustrates a sequence of experimental trials in an experiment of action understanding. The images represent the final frame (and action state) in short videos that subjects observed. Within the videos, action means and outcomes were independently repeated. The second and third rows illustrate the predicted neural and fMRI BOLD responses in regions of the brain that decode means and outcomes, respectively. According to the principles of repetition suppression, regions that decode the means of an action should show greater activity on the first and last trials, in which the means of executing the action (pushing and pulling the lantern handle) are novel with respect to the previous trial. These same regions should show reduced activity on the second and third trials, in which the means are repeated. Regions that decode outcome should show greater activity on the first and second trials, in which the outcome of the action (lantern turns off or on) is novel. These regions should show decreased activity on the third and fourth trials, in which the outcome is repeated. By identifying distinct areas of the brain that respond according to unique predicted response profiles such as these, neural modules for specific aspects of action representation can be distinguished.

interactions during motor execution (Binkofski et al., 1998; Frey et al., 2005) and lesions to this area disrupt grasp formation (Binkofski et al., 1998; Frak et al., 2006). In addition, transient disruption with transcranial magnetic stimulation of this area in healthy subjects alters hand reshaping or orienting when the object properties change after movement onset (Rice et al., 2006; Tunik et al., 2005).

The localization of object-centric goal related activity to left aIPS during grasp observation has been replicated and extended in numerous RS fMRI studies. Goal related activity in aIPS can even be detected when the observer watches triangles on a computer screen "grasp" other triangles (Ramsey and Hamilton, 2010b). The specificity of aIPS for representing goal related activity is further supported by contrasting this function with other "means", including grip type (Hamilton and Grafton, 2007), target identify (without grasping) (Ramsey and Hamilton, 2010a; Shmuelof and Zohary, 2005), target location (Ramsey and Hamilton, 2010a), target status (cup empty or full) (Ramsey and Hamilton, 2010a) and the identity of the agent performing the action (Ramsey and Hamilton, in press; Shmuelof and Zohary, 2006). All these other characteristics of an action are localized to brain regions other than aIPS. Thus, means and object-centered goals are consistently dissociable at a functional anatomic level. Further evidence that aIPS is specific to object-related goals can be deduced from an RS fMRI study in which intransitive goal oriented actions were observed. In this case there was no localization of goal effects to aIPS (Lestou et al., 2008). Putting these studies together, there is now good evidence that the aIPS region forms a critical node within a larger functional network for decoding action. It plays a supraordinate role in decoding action intention based on hand–object interactions, drawing on evidence decoded in functionally subordinate systems.

Object knowledge

Artifacts can carry specific information about how a hand could plausibly interact with an object during grasping (Valyear et al., 2007). In fact, observers cannot easily ignore the inherent manipulability of an object (Handy et al., 2003), even when the identity of the object has no bearing on how the motor act is performed (Bach et al., 2005). Functional knowledge can be assessed in patients with visual extinction as well as healthy subjects while they are observing more than one moving object. An observed movement of objects will be perceived as an action rather than just isolated movement, only when the movement is temporally, spatially and functionally appropriate for the deduced action (Green and Hummel, 2006; Riddoch et al., 2003).

It has been proposed that actions are remembered as preformed motor patterns that could be used to solve specific tasks. An example would be selecting an appropriate hand grasp related to an object. The set of these associations would form an action vocabulary. The interplay between knowledge of an object's functionality and associated action vocabularies that match this function has been tested in a number of ways. In fMRI subtraction experiments brain areas associated with decoding how an object is manipulated (inferior parietal lobule) are essentially the same as those used for retrieving conceptual or categorical knowledge of an object (Boronat et al., 2005; Chao and Martin, 2000; Johnson-Frey et al., 2005). There is growing evidence that the left IFG also plays an essential role in storing action vocabularies (Johnson-Frey et al., 2003). RS fMRI has been able to make additional headway into this distinction. In one experiment, subjects watched either of two objects being grasped with either a power or precision grip. Areas sensitive to how an object was grasped included bilateral inferior lateral occipital cortex, left intraparietal sulcus and left IFG (Hamilton and Grafton, 2007). A lesion in IFG will also cause a deficit in the decoding of non-linguistic pantomimed actions (such as licking something) with appropriate objects (an ice cream cone) (Saygin et al., 2004a). Studies of patients with limb apraxia have also examined gesture comprehension deficits, including intransitive gestures. These suggest that there is an anatomic overlap for the neural substrates of gesture production and comprehension (Ferro et al., 1983; Heilman et al., 1982; Rothi et al., 1985). Precise lesion localization shows that the lesions are consistently left-lateralized with damage to the opercular and triangularis portions of the IFG (Buxbaum et al., 2005; Pazzaglia et al., 2008). Virtual lesions created by disruptive transcranial magnetic stimulation in normal subjects also build a case for the use of inferior frontal cortex in supporting action vocabularies during both execution and comprehension. TMS to inferior premotor cortex impairs judgments in the weight of an object another person is lifting and also leads to increased response times in a delayed match to sample task when the matching is for body actions (Pobric and Hamilton, 2006; Urgesi et al., 2007). These real and virtual lesion data suggest that inferior frontal cortex, particularly in the left hemisphere may be particularly important for the storage or retrieval of action vocabularies, that is, the relations between known body movements and their probable meaning in terms of action consequences. The involvement of premotor areas also raises the intriguing possibility that one of the possible mechanisms for deriving meaning is via some form of motor simulation, where an observed behavior is "played out" in one's own motor system through a matching process (Rizzolatti, 2005).

End state and context

In natural behavior the grasping of an object is rarely the final goal of an action. Instead, this represents an intermediate step followed by object manipulation leading to a change in the end state of the object or environment. Furthermore, actions are performed in natural contexts that influence the range of expected intentions an observer might expect an agent will perform. Here it is argued that the processing of an action's end state and its context rely on closely interacting brain networks. Brain localization for the end state of an action was first tested in an RS fMRI study. Changes in an object's outcome (e.g. an open or closed box) were varied independently of changes in how the object was manipulated (e.g. pushing or pulling on the box lid) (Hamilton and Grafton, 2008). Based on the RS effect, final outcomes were linked to strong bilateral pattern of activity in IPL and IFG as well as modest activity in left aIPS, the area observed when the object itself was the goal. The findings suggested that as the goal shifts to an outcome rather than just an object the functional substrates also broaden to bi-hemispheric recruitment requiring greater parietal cortex involvement. This example demonstrates that as intentionality is inferred, there is an increasing recruitment of the right hemisphere. Another way to frame this finding is to propose that the left hemisphere is more closely linked to action means, whereas the right hemisphere is linked to the intentionality of the agent performing those means. Expanding on this hypothesis, a split brain patient was asked to watch a sequence of static pictures of an agent manipulating one object (pitcher of water) to achieve a familiar goal (fill a glass of water). Picture sequences showed successful outcomes or failures. Response times showed a double dissociation between the responding hand and the question posed to the patient (Ortigue et al., 2009a). The left hemisphere showed greater sensitivity when responding to how an action was performed and the right hemisphere to why an action was performed (did the agent intend to achieve this outcome).

The rationality of an action is judged not only by the relationship of biological motion and target object but also by the larger context within which the action takes place. Context can be manipulated experimentally by adding other objects that determine the functional state of the target object or that serve as obstacles or distractions (Schuch et al., 2010). For example, expectation of how a coffee cup will be picked up is determined in part by whether the meal is beginning or has ended and the table is being cleared. The presence of this contextual information leads to a greater activity in the AON, particularly in the right hemisphere (Iacoboni et al., 2005). Many studies show that the posterior STS and adjacent MTG region are not only sensitive to biological motion, but also to the contingent relationship between the action and constraints determined by other objects and barriers. There is increased MTG activity when there is a violation of the expected movement pattern in relationship to obstructions (Jastorff et al., 2011). We expect a subject to reach around a barrier to a goal, but not too far around a barrier. That is, there is a tight mapping between context and expected actions. STS and MTG regions are highly sensitive to this mapping.

Many actions can take a form in which the surface features of motion, objects and agent do not reveal an obvious intention. Or, the observed action is so deviant from the expected behavior given the context that the rationality of the agent might even be called into question. There is increasing evidence that as the range of plausible actions and thus the complexity of action inference increases, the observer draws on additional brain networks, including a set of regions now referred to as the "social network" (S-N). The S-N includes amygdala, insula, medial prefrontal and posterior temporal cortex (overlapping with the AON). It is active in theory of mind tasks and social interaction. It is thought to be essential for inferential processes of rationalization and mentalization of other agents (Wheatley et al., 2007). Thus, for novel actions or actions out of context, or actions performed by people of a different race, the observer may shift to an inferential interpretive system (Liew et al., in press; Spengler et al., 2009). To give an example, in one elegant study, subjects observed an agent turning a light switch on with their leg (Brass et al., 2007). Under normal conditions, this is an implausible behavior and there is greater activity of the S-N. However, if the agent's hands are full, the behavior is plausible. The AON was active across both plausible and implausible conditions.

Action semantics

The relationship between action and language is complex, and empirical findings regarding this relationship depend in part on the experimental approach one adopts. From the perspective of patient studies it is possible to clearly dissociate language and action processing by demonstrating selective impairments in one domain or the other (Buxbaum et al., 2005; Buxbaum et al., 2006). On the other hand, there is a general consensus based on interference and functional imaging that there are at least some shared substrates in the brain for supporting language and action. In fact, it is becoming increasingly difficult to create sharp functional boundaries between these two cognitive domains. A few examples: simply reading about an action verb will modulate excitability of the motor cortex (Hauk et al., 2004; Hauk et al., 2008) and reading about body actions will recruit both the posterior STS including the extrastriate body area (Deen and McCarthy, 2010) as well as motor cortex in a somatotopic manner (Boulenger et al., 2009). The degree to which different types of words influence action systems remains a moving target. These effects appear to be stronger when entire sentences involving a body action are read, rather than single words such as action verbs, suggesting that the sensorimotor system is used in part to decode meaning in high-level semantics for both observed and read behavior (Willems et al., 2010). Given this involvement of sensorimotor systems in decoding semantics, it is interesting to ask if action understanding has a semantic structure akin to language. This can be tested in part by identifying intersections in action and language processing. One approach is to determine if the functional anatomy distinguishing part–whole structure detected during action observation is also present in reading tasks. As an example, in one study subjects read during fMRI and there was greater activity in IPL when they mentalized parts that determined how an action should be performed (means) and greater activity in PMv and MTG for statements that were directed toward the larger goal of why an action was to be performed (ends) (Marsh et al., 2010). Recruitment of the AON, particularly IPL, is greater for concrete and metaphorical statements compared to abstraction sentences (Desai et al., in press). In contrast, STS correlates with increasing language abstraction.

What these different imaging experiments convincingly demonstrate is that there is a well-defined network for decoding actions extending through temporal, parietal and frontal cortex. The network is modular, hierarchically nested, and capable of expanded recruitment as tasks become increasingly abstract. For decoding of means, there is a left hemispheric predominance and as the decoding process incorporates more information related to outcomes this recruitment is bilateral. The AON is intertwined with language systems and scalable in the sense that increasing complexity or socially relevant contextual information extends brain recruitment to areas associated with inferential reasoning. These properties of hierarchical processing, sensitivity to action semantics and responses highly sensitive to action goals should be expected in at least some of the studies of action understanding using electrophysiologic methods.

Physiologic signatures of action understanding — evoked potentials

We are currently in the midst of an explosion of new discoveries relating changes of electromagnetic activity measured over the scalp with the "work" of observing and interpreting other people's actions. In the following section and Table 1 we highlight some of these discoveries, focusing on just those potentials, rhythms and microstates that have been demonstrated to have properties sensitive to the decoding of observed actions. As sensing methods and analysis evolve they provide targets of opportunity for creating neuroergonomic solutions to intention decoding.

Readiness potential

The first electrical potential to be measured was the readiness potential (Kornhuber and Deecke, 1965). As a subject initiates a volitional movement, there is a slow progressive increase in negative voltage over the central scalp. Later work demonstrated that under cued conditions, when subjects prepare a movement for a specific hand, the readiness potential moves to the hemisphere contralateral to the moving hand close in time to the onset of movement; the lateralized readiness potential (LRP) (Vaughan et al., 1968). Analogous changes can be observed with magnetoencephalography (MEG) by detecting the readiness field (RF) and lateralized readiness field (LRF) (Deecke et al., 1982). Source localization using modern MEG and EEG methods suggests the RP/RF arises from the supplementary motor area and the LRP/LRF from the sensorimotor cortex.

Given the extensive imaging and TMS evidence for recruitment of motor areas in language tasks, it is relevant to ask if the RP or LRP is also sensitive to cross talk from language processing. In one test for this, an arm reaching task was combined with auditory word presentation. The words included action verbs as probes. They were presented too fast for conscious perception so that subjects would not inadvertently imagine performing any of the actions. Changes in the RP revealed that subliminal displays of action verbs during movement preparation reduced the RP and changed the kinematics of the subsequent reaching movement (Boulenger et al., 2008). This provides further evidence that the motor cortical structures have a broad function that spans preparation, execution and action language processing. It is logical then to probe if action observation would also modulate the RP. As subjects waited to observe a hand grasping an object the RP was modulated in anticipation of the temporally predictive event (Kilner et al., 2004). Control trials established that this anticipatory response was not linked to an expected stimulus, but to an expected action. The LRP response in contralateral cortex is also modified during observation of another agent's action. In one study, it was sensitive to the correctness of the actor's response (van Schie

Table 1
EEG/MEG signatures of action understanding.

Marker	Typical usage	Putative source	Action observation event	Potential utility
Readiness potential filed	Increased negative voltage mainly in central electrodes during movement preparation	Supplementary motor area	Anticipation of expected action event	Predicting when an action will occur
Lateralized readiness potential filed	Increased negative voltage in lateral frontoparietal electrodes during cued movement preparation	Sensorimotor cortex	Movement of a hand; correctness of movement	Detecting when a simple action event has occurred
N400	Negative potential fron 250–500 post stimulus. Reflects difficulty of integrating stimulus into preceding semantic context	Widespread sources, L STS	Violotion of action semantics based on preceding action events or contexts	Marker of unexpected behavioral outcome or action given a context
P600	Positive potential beginning 500–600 post stimulus. Reflects syntactic errors and garden path reanalysis of language	Posterior temporal lobe	Violation of expected action goals	Marker of unexpected action goals (garden path reanalysis of action)
Beta	12–30 Hz modulation occurring with control of volitional movement	Motor cortex	Modified during observation of simple discrete finger movements	Marker of simple movement events
Alpha	8–12 Hz modulation with increased internal “focus” executive control, attention	Thalamic pacemakers	Decrease in anticipation of an observed movement	Marker of anticipation
Mu	8–13 Hz suppression with performance of motor acts	Bilateral sensorimotor cortex	Somatotopically specific attenuation during observation of body movements and simple goal directed actions	Marker of ongoing movement
Microstate	Localization of spatially stable voltage over the scalp	Bilateral posterior temporal and parietal cortex	Earlier and prolonged microstate in right parieto-temporal with ambiguous actions	Detecting ambiguous hand-object actions; detection of contextually ambiguous actions
Microstate-RS	Localization of spatially stable voltage over the scalp. Changes in the number or duration of microstates with repeated presentations of a stimulus	Bilateral posterior temporal and parietal cortex	Detection of intention-specific hand–object interactions as early as 60 ms post object contact	Detecting intentions with hand–object interactions

Abbreviations:
ERD — event related desynchronization.
RS — repetition suppression.

et al., 2004). However, in this case the potential associated with correctness was located more posterior to the classic response over motor cortex. The LRF measured with MEG during action observation was tested with observations of a contralateral hand movement. Unlike the classic LRP it arose much more quickly and was insensitive to correctness of the observed movement (van Schie et al., 2008). Additional studies will be needed to distinguish the timing and localization of the LRF in relationship to observed actions. Both the RP and LRP hold promise as potential EEG markers for the implicit detection of action events, predicting when they might be temporally expected to occur, and for assessing correctness of ongoing actions.

N400

The N400 is characterized by a distinct pattern of scalp electrical activity with a negative component that peaks around 400 ms post-stimulus onset, in the time window ranging from 250 to 500 ms. Initially characterized in auditory language studies, the N400-component is widely accepted as a measure of the difficulty of integrating a new stimulus into the surrounding semantic context (Kutas and Hillyard, 1980). Putative localization of the N400 suggests it emerges from widespread sources (Kutas and Federmeier, 2000), with some predominance to the left STS based on MEG, (Halgren et al., 2002), intracranial event related potentials (ERPs), (Guillem et al., 1995) and MEG/MRI, (Simos et al., 1997) with additional contributions from the right temporal lobe (Van Petten and Luka, 2006). The conditions where an N400 emerges have been generalized to include tasks involving reading about action. The sequential nature of action creates anticipation about the conclusion or expected outcome of the action. Thus, there will be a more prominent N400 when a participant listens to a sentence describing an action with an unexpected as opposed to an expected outcome. N400 studies also show that there is a coupling between motor behavior and language semantics. When a subject is asked to judge a sentence that describes an action of a hand, and simultaneously use their own hand to make a response when they understand the sentence, the N400 increases in amplitude when the actual hand posture is incongruent with the action being read (Aravena et al., 2010).

A critical point is that similar N400 results are observed when the sequential nature of the action is created not with words but with pictures or video (Reid et al., 2009; Reid and Striano, 2008). Whenever any of these modalities follow the same sequential structure and include unexpected violations of action semantics there will likely be an N400. For example, the N400 is observed when sequences of words are followed by congruent or incongruent gestures (Wu and Coulson, 2005). N400 responses to photographs with unexpected action outcomes are delayed in latency and more anterior in topography when compared with N400 components derived from language studies, potentially due to the complexity of the visual stimulus (Reid et al., 2009). The N400 also discriminates between contextually appropriate and inappropriate objects that are observed in video film clips of common activities (e.g., for shaving, a rolling pin is used instead of a razor) (Sitnikova et al., 2003). The onset of this potential occurs shortly after object presentation, indicating that semantic integration is a rapid online component of real-world perception. Follow-up studies show that it is not just a mismatch between object and action, but the full relationship between the context, action and tool that modifies the N400 component (Sitnikova et al., 2008). A similar effect of context can be observed when hand gestures are used instead of objects (Gunter and Bach, 2004).

The above studies emphasize the common occurrence of the N400 in tasks where action has a semantic structure and there is an unexpected event. In general, the topography and timing of the potentials are consistent across experiments. Only one study has directly tested whether different types of action semantic errors have separable N400 potentials (Bach et al., 2009). This study drew on the idea that understanding tool use depends on both the particular motor action that is performed and on the known function of the given tool. These two components of action semantics were dissociated by presenting two consecutive pictures. The first one showed a hand holding a tool in a given orientation and the second added a potential target for the held tool. Two mismatches are possible in the second picture. An orientation mismatch would occur when the tool position was not consistent with the required insertion (a screwdriver not aligned with the groove in the target screw). A functional mismatch would occur when the tool being used was inappropriate for the target (a screwdriver being inserted into a door lock). While both these mismatches modulated the N400, close analysis revealed differences in the timing and spatial distribution of the potential as a function of mismatch property. The differential structure of the N400 component across these two types of unexpected action events suggests that the decoding of how a tool is used is separable from the decoding of what it is used for. This is analogous to the imaging and split-brain patient behavior experiments that differentiate the "how" and "why" in action understanding based on hemispheric lateralization. The conceptual distinction of decoding what is done and why an action is being performed remains an important target for future neuroergonomic experiments.

P600

The P600 is an ERP first observed in language studies (Osterhout and Holcomb, 1992) and elicited by hearing or reading grammatical errors and other syntactic anomalies; for example, "The man drop the eggs". It is also elicited when reanalysis or repair are required, as in garden path sentences where the listener parses a sentence on the fly in one form when in fact the full sentence has a different meaning (Friederici, 1995). For example, "The farmer persuaded to sell the pig was fat". The P600 is a positive deflection with an onset around 500 ms and reaches a peak around 600 ms after presentation of the eliciting stimulus, which can last several hundred milliseconds. It typically appears on central and parietal electrodes but can also appear more frontally. Source localization by MEG has suggested that the generators of the P600 are in the posterior temporal lobe, and more so in the left hemisphere (Service et al., 2007). Additional language studies show that it is also modulated by violations of goal-related requirements of actions described linguistically (Hoeks et al., 2004; Kolk et al., 2003; reviewed by Kuperberg, 2007). Given the interplay of action descriptions and linguistic syntax, it is relevant to ask if there is an analogous marker of syntactic processing of observed actions. Only a few action observation studies have even reported P600 ERPs and their interpretation remains uncertain. One study in support of this presented movies where target objects at the movie endings violated requirements of action-goals defined by the context. For example, an electric iron was used instead of a knife in a bread cutting task. In addition to an N400, a posterior P600 was observed and interpreted as related to the ongoing processing of information against the task requirements of the observed actions (Sitnikova et al., 2008). In both cases, it is possible that semantic rather than syntactic violations were the basis of the P600. Unlike the N400 literature, action studies with the P600 remain fairly limited and it will take time to determine if there is potential utility with this marker of brain activity.

Event related changes of voltage synchrony

Beta

The beta rhythm designates a frequency range of human brain electromagnetic activity between 12 and 30 Hz. Low amplitude beta waves with multiple and varying frequencies are typically associated with active, busy, or anxious thinking. Over the motor cortex beta waves are intimately associated with the control of movement. They appear in isotonic movements and are suppressed prior to or during movement changes (Baker, 2007). Bursts of beta activity are associated with a strengthening of sensory feedback (via peripheral nerve stimulation) in static motor control (Lalo et al., 2007) and they are increased when movement has to be resisted or voluntarily suppressed (Zhang et al., 2008). Localization to motor cortex is supported by invasive recordings of neurons of non-human primates showing synchronous oscillatory activity in this range (Baker et al., 1997; Murthy and Fetz, 1992) and by MEG source localization in humans (Kilner et al., 2000; Salmelin and Hari, 1994). Given this interplay of beta rhythm modulation and motor activity, influences on the beta rhythm by action observation have also been sought out. Using MEG, an early seminal experiment compared activity while subjects manipulated a small object and while they observed another individual performing the same task. Peripheral nerve stimulation was used to excite motor cortex and task specific modulation of poststimulus rebound of the beta rhythm over motor cortices was quantified. The beta rebound was strongly suppressed bilaterally during object manipulation. The rebound was also modulated during action observation, but not as dramatically. Control experiments, in which subjects were instructed to observe stationary or moving stimuli, confirmed the specificity of the suppression effect (Hari et al., 1998). In a related study, event-related desynchronization (ERD) and synchronization (ERS) of beta rhythms in association with the execution (with visual feedback) and observation of brisk unilateral right and left aimless finger movements were tested. Under both conditions, ERD peaked during both movement execution or observation and was replaced by an ERS "rebound" or "recovery". Similar topology for ERD and ERS in central scalp regions was observed overlying premotor/primary sensorimotor cortex (Babiloni et al., 2002). In an important follow up MEG experiment, the subjects tapped on a drum, listened to the tapping or watched the tapping. The level of the beta rhythms over contralateral motor cortex initially decreased about 2 s before the action and then increased, with a rebound occurring 0.6 s after the tapping ceased. A very similar time course occurred during observation starting approximately 0.8 s before the action and was also followed by a rebound. When the subject just heard the tapping sound there was no beta modulation except for a rebound after the sound (Caetano et al., 2007). In a third study, subjects observed arm movements and again, there was a significant modulation of beta oscillations overlying left and right sensorimotor cortices. In this case the pattern of attenuation was driven by the side of the screen on which the observed movement occurred and not by the hand that was observed to be moving (Kilner et al., 2009). Together these establish a remarkable signature of motor cortex reactivity during action observation of discrete simple motor events.

Alpha rhythms

This scalp activity occurs in the 8–12 Hz range and is considered to arise primarily from synchronous and coherent activity of thalamic pacemaker cells (Palva and Palva, 2007). It is enhanced during many internalized tasks, such as mental calculation, meditation and working memory. The rhythm can also reflect inhibition of task-irrelevant cortex and also contributes to active control of attention and consciousness. The alpha rhythm in adults is attenuated bilaterally during execution of a grasping action (Hari and Salmelin, 1997). During action observation, it decreases in advance of the observed action, demonstrating it is linked to anticipation of a motor act (Babiloni et al., 2002; Southgate et al., 2009).

Mu rhythms

The mu rhythm covers a frequency range of (8–13 Hz) and is typically localized over bilateral sensorimotor cortex. It is strongly and symmetrically suppressed during the performance of contralateral motor acts. Modulation of the mu rhythm likely reflects the synchronization of pyramidal neurons of the motor cortex. Gastaut first observed that mu rhythm desynchronization also occurred while his subjects observed actions executed by someone else (Gastaut and Bert, 1954). In patients undergoing intraoperative recording by electrode grids there was suppression of mu rhythms during action observation that was somatotopically organized, corresponding to the body part moved by the actor (Arroyo et al., 1993). Even degraded images of action based on point-light biological motion will attenuate the mu rhythm (Ulloa and Pineda, 2007). More recent studies show that the degree of mu rhythm suppression is greater for goal oriented actions (grasping an object) compared to intransitive actions (an open grasp without an object) (Muthukumaraswamy et al., 2004) and this goal sensitivity emerges in childhood (Lepage and Théoret, 2006; Nyström, 2008) and is experience dependent. For example, musicians will show a greater mu rhythm modulation when watching someone play an instrument compared to non-musicians (Behmer and Jantzen, 2011; Hadjidimitriou et al., 2010).

Microstates

While conventional EEG analysis focuses on event related waveform or frequency analysis at certain electrode positions it is also possible to identify brain microstates — time intervals in which the spatial distribution of scalp electrical activity is stable (Brandeis et al., 1995; Lehmann et al., 1994). This is an analytic approach where consistent distributions of scalp voltage or current are grouped into temporal bins using statistical clustering algorithms (Murray et al., 2008). Once these stable periods of activity are identified then task differences in microstate duration or global field power can be compared. In addition, the putative sources for the different microstates can be localized with any one of a number of available inverse solutions. In studies of action understanding microstate analysis has mainly been used to look at the time course of visual evoked potentials that contain information about the content of observed actions. Here we focus on two examples.

In one microstate experiment of action understanding, the effect of hand interaction with a given object and the influence of context on the temporo-spatial dynamics of EEG activity over the scalp were assessed (Ortigue et al., 2010). Participants observed a sequence of pictures of the hand of an unseen agent grasping an object in typical or unexpected postures, with or without contextual information surrounding the target object (grasping an iron vs. grasping an iron on an ironing board with clothes in need of ironing or already ironed). Microstate analysis time-locked with the frame showing the hand–object interaction revealed a rapid evolution of localized processing across temporal and parietal cortices. The localization was initially in bilateral posterior cortical activations with a strong activation of the left posterior temporal and inferior parietal cortices followed by a significant increase of the activations of the right temporo-parietal region with simultaneously co-active left hemispheric sources. Ambiguous hand actions as well as object-context mismatches led to an earlier shift and more prolonged microstate with sources in the right hemisphere. The findings are generally consistent with experiments from fMRI suggesting that there is an initial decoding of the means of an action within left tempo-parietal cortex that shifts to the right hemisphere over time. Uncertainty of context or intention (elicited by ambiguous hand actions) leads to an earlier and prolonged recruitment of the right hemisphere sources, suggesting they are recruited to assess the ends or intentionality of the actor.

In a more elaborate EEG microstate experiment, the spatiotemporal dynamics of action understanding were analyzed in relation to the type of grasp that was used to accomplish an action goal. The approach was motivated by prior RS-fMRI studies (described above) demonstrating strong suppression of aIPS activity when the grasp was repeated on the same object. In this case, RS-EEG was employed. Furthermore, to decouple the effect of object as goal and hand action as the goal, different grasps and objects were used (Ortigue et al., 2009b). Participants watched movies of the hand of an unseen actor reaching and grasping a gun or hair dryer with a grip allowing them to squeeze the trigger or engage the "on" switch in an intention of using the tools or with a grip allowing them to pick the object up. Thus, the effect of repeating the intended function (determined by the type of grasp) could be assessed independently of the object that was grasped. Other aspects of the action including object location, object orientation and hand to be used were independently manipulated so that intention could be distinguished from these low-level visual features. The EEG data was time locked to the moment the hand touched the object. EEG global field power was significantly reduced with repeated intentions at a very early time (starting at 60 ms) and again at a later (330 ms) period. Source localization during these two intervals demonstrated stable microstates involving the right STS and aIPS, highly consistent with RS localization measured by fMRI acquired in the same subjects. These results reveal the dynamics of intention decoding in both temporal and parietal cortex at multiple stages of processing. The results provide a putative lower bound of approximately 60 ms after object grasp for detecting specific hand–object evoked responses that could potentially be used in neuroergonomics applications.

Conclusion

The neuroergonomic approach integrates naturalistic task demands with methodologies and insight from cognitive neuroscience. The ultimate goal is to enhance performance through changes in training or the modification of information processing in real time using neural signatures. In this review, we show that there are well-defined neural substrates for action decoding that form the basis for well-structured hierarchical processing across temporo-parietal and to a lesser degree, frontal cortex. EEG and MEG studies resonate this hierarchical view with source localization frequently reflecting what is observed in functional imaging. While no EEG method is currently able to read a person's mind or to reveal what they are looking at, it is clear that there are a number of EEG markers that are dependent on general properties of the decoding process. To date, the most dramatic of these is the N400, which captures inconsistencies between expected action structure and outcomes. Admittedly, an application using something like this will require significant effort and time to create. Nevertheless, the rapid evolution of single trial EEG acquisition and analysis suggest that this is well worth pursuing. Major enhancements in signal processing, either through independent component analysis or other techniques will likely be needed to leverage this response at the single trial level of analysis. In parallel, the relative specificity and utility of EEG markers in relationship to action decoding are sure to evolve. With these improvements we can expect that over a longer time horizon, neuroergonomics could impact action understanding in additional applications. These include: (1) development of sensor systems and analysis streams for brain–computer systems to augment or accelerate an observer's decision making; (2) creation of training tools, including immersion, that shape the observer's performance based on brain responses; and (3) the evolution of monitors, workstations and work environments to adapt information to features that the observer depends on.

Acknowledgments

This work was funded by the Institute for Collaborative Biotechnologies through contract no. W911NF-09-D-0001 from the U.S. Army Research Office, Public Health Service grant NS44393 and the James S. McDonnell Foundation.

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