selection, preparation, and monitoring: current approaches to studying the neural control of action

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imagine an athlete throwing a disc, as shown on the cover of this issue. we see him tensing his muscles but how can we know which brain structures control this powerful action? the ancient greeks could only observe and measure limited, external aspects of this movement, such as the timing of muscle flexions and the distance the discus is thrown. just as the ancient greeks, until recently we had little way to observe the brain mechanisms that give rise to this feat. since movements were considered to be difficult to transfer to the laboratory to provide quantitative data, the study of movement has for a long time been one of the less studied fields of cognitive psychology. the rise of various techniques to study the human brain during task performance initially seemed to aggravate these problems, as they all require the participant to remain motionless for an extended period and are highly sensitive to movement artifacts. as such, the study of movement has long been a neglected child in the realm of cognitive neuroscience. over the last 15 years, however, this situation has changed. this is due in part to the rise of various imaging techniques and accompanying statistical tools that are less sensitive to these problems, but also to the increasing interest in the cognitive processes associated with any movement. instead of focusing on the movement directly, this research is focusing on the processes leading up to the movement and the evaluation of the consequences of the movement following its execution. all these processes that precede and directly follow observable movements are nowadays collectively referred to as actions. these developments, in turn, have led to a large rise in popularity of action-related research. the goal of this special issue of cortex is to illustrate the diverse experimental approaches currently employed in studying the neural control of actions and the consequences this is having on other domains of cognitive neuroscience. the contributions in this issue constitute a mixture of reviews and novel experimental data. the papers partly originate from a symposium on this topic held at the radboud university nijmegen, november 9–10, 2006.

the techniques most often used to probe neural activity during selection, preparation, and monitoring of actions include various signals derived from eeg and meg, such as the event-related potential (erp), motor-evoked potentials in the electromyogram elicited using transcranial magnetic stimulation (tms), and imaging techniques such as positron emission tomography (pet) and functional magnetic resonance imaging (fmri). by necessity, the overt movements that can be performed by participants in these experiments are limited. eeg signals are highly sensitive to movement artifacts, as are images obtained with fmri. although recently solutions have been found to study more complex movements in the fmri environment (diedrichsen et al., 2005; majdandzic et al., 2007; rémy et al., 2008, this issue), the movement studied is often nothing more than a simple button press. however, a number of paradigms have been proposed that allow imaging of the representations underlying actions uncontaminated by the execution of complex movements (jeannerod, 2006). for instance, a window on the neural processes underlying action specification can be provided by studying imagery of these actions (de lange et al., 2008, this issue) or the preparation of actions. these paradigms allow the researcher a window on processes far more complex than the simple execution of
a button press by focusing, for instance, on the transformation of information from abstract stimuli into a motor response (Mars et al., 2008, this issue) or the preparation of different sequences of simple movements based on different types of prior information (Gladwin et al., 2008, this issue). This type of paradigm has now been used in combination with a number of research modalities, including fMRI (Toni et al., 1999; Mars et al., 2008, this issue), TMS (Van den Hurk et al., 2007; Sinclair and Hammond, in press), and measures derived from EEG, such as ERPs and, more recently, oscillatory EEG responses (Gladwin et al., 2008, this issue).

Apart from studying the processes leading up to movement, studying the evaluation of the consequences of actions has become very popular over the last decade, leading to the separate subfield of action monitoring. This subfield provides a prime example of use of a convergence of neuroimaging techniques to study a common problem. Action monitoring became popular following the discovery of the error-related negativity (Falkenstein et al., 1990; Gehring et al., 1993), a component of the event-related brain potential that is elicited following the detection of performance errors in choice reaction time tasks. Subsequently, fMRI studies have localized the source of this component in the anterior cingulate cortex in the medial frontal cortex (Carter et al., 1998; Holroyd et al., 2004; see also Zanoli et al., 2008, this issue). Moreover, studies in patients have focused not only on their behavioral consequences, but also on the results of neural impairments on neural markers of action monitoring (e.g., Ulspenger and Von Cramon, 2006). Importantly, this field has a strong focus on comparing the experimental results with the predictions of formal computational models of neural processes (Botvinick et al., 2001; Holroyd and Coles, 2002; Holroyd and Coles, 2008, this issue).

Although the study of patients with brain damage has traditionally been one of the few available methods of investigating the necessity of brain regions for movement execution, here we can also see an increasing emphasis on disorders in the higher-order cognitive aspects of action in patients with brain lesions (Freund et al., 2005; Blangero et al., 2008, this issue). Importantly, action-related research is now finding its way to a broad range of clinical populations. One prime example of this is the study of motor imagery in patients with conversion paralysis (De Lange et al., 2008, this issue). The relatively simple tasks and the strong neural correlate of neural processing found in the error-related negativity have served to make action monitoring research easily transferable to clinical settings. The field of psychiatry has adopted this particular aspect of action-related research, focusing for example on deficits in performance monitoring in patients diagnosed with schizophrenia, borderline personality disorder, and major depressive disorder (Schrijvers et al., 2008, this issue).

A prime example of the far-reaching consequences of action research is the current trend to view higher cognitive abilities as being reliant on the brain’s action system. Some scholars try to account for some of these abilities by virtue of automatic mappings between sensory and motor data (Rizzolatti and Craighero, 2004). Other authors try to find a difficult compromise between these reflex-like views of the human brain and the apparently different level of processing complexity associated with functions involving conceptual reasoning or mentalizing, to just name a few (Haggard et al., 2007). It is also conceivable that evolutionarily preserved processes like those involved in motor control might be strongly influenced and exploited by new layers of cognitive processes (De Ruiter et al., 2007). Irrespective of the particular theoretical position one assumes, the predictive and explanatory values of a given account need to be grounded on the neural mechanisms that mediate actions. De Bruijn et al. (2008, this issue) provide an example of this approach, extending a well-known speeded-response paradigm to the domain of social interaction.

As already alluded to above, a main focus of modern cognitive neuroscience research is the integration of data obtained using different experimental techniques. Medendorp et al. (2008, this issue) show how sophisticated behavioral experiments and functional imaging experiments can be used to provide complimentary pictures of the processes underlying spatial coding and action planning. Furthermore, since the precise neural basis of most experimental techniques is still not fully understood and is an area of ongoing research (Van Elswijk et al., 2008, this issue), combining different imaging modalities may allow a more unbiased view of neural processes. The large body of data on the neural processes underlying actions in nonhuman primates and the relative ease with which the motor system can be reached by experimental techniques such as TMS make action research one of the first domains in which such a combined approach is explored. This can be achieved by running related experiments in different modalities, such as illustrated by the contribution of Zanoli et al. (2008, this issue), who focus on fMRI and ERPs. A further step is to combine different approaches in the same session, such as illustrated by recent studies combining EEG and fMRI (Debener et al., 2006), TMS and fMRI (Bestmann et al., in press), and EEG and TMS. O’Shea et al. (2008, this issue) provide an overview of this type of work in the domain of action.

We hope that the readers will find this special issue of Cortex an inspiring overview of how different techniques and paradigms can be used together to provide a more complete insight into the neural processes underlying actions and their application in the cognitive neurosciences. Furthermore, we hope it gives the reader a sense of how research into the neural processes underlying action can be beneficial to new areas of cognitive neuroscience, such as social neuroscience and psychiatry.

Acknowledgements

We are grateful to Cortex’ editor Sergio Della Sala for providing us with the opportunity to edit this special issue and to Cheryl Phillips for her excellent editorial assistance. The symposium ‘Selection, preparation, and monitoring of actions’ was made possible by generous contributions from the Dutch Organization for Scientific Research (NWO) and the Nijmegen Institute for Cognition and Information (NICI) at the Radboud University Nijmegen. RBM is supported by a Marie Curie Intra-European Fellowship within the 6th European Community Framework Programme.
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