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The role of the preSMA and the rostral cingulate zone in internally selected actions

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In everyday life, one can differentiate between actions that are primarily internally guided and actions that are primarily guided by external events. FMRI studies investigating the neural correlates of internally guided actions usually report activation maxima in the rostral cingulate zone (RCZ) as well as the preSMA. However, the pertinent contrasts were often confounded by perceptual and motor differences between the different conditions. In the current study, we reinvestigated the neural correlates of internally vs. externally selected actions using a paradigm that avoids any such perceptual or motor confound. By doing so, we wanted to address the yet unsolved question which differential role the preSMA and RCZ play in internally guided actions. Subjects were required to make left or right key presses at the midpoint between isochronous pacing signals (a sequence of 'X's presented to the left or the right of the fixation point). In the internally selected condition, the location of the 'X' was determined by the location of the preceding key press that the subjects selected freely. In the externally selected condition, by contrast, the location of the 'X' prescribed the location of the subsequent key press response. We found that the RCZ was differentially activated by internally as compared to externally selected actions. In contrast to previous studies, the preSMA showed equal activity in both conditions and thus did not differentiate between the two modes of action selection. This suggests a primary role for the RCZ in internally selected actions.

Keywords: fMRI; Internally selected action; Externally selected action; RCZ; PreSMA

Introduction

In everyday life, actions are either more internally guided, for example switching on TV to watch the news, or they are more externally guided by environmental stimuli, for example stopping in front of a red traffic light. Voluntary, internally guided actions are not prompted by external cues, but rather guided by intentions. An internally guided action commonly helps the agent to produce a desired effect in the environment (Prinz, 1997). According to the ideomotor theory, voluntary action control is based on learned associations between movements and their perceivable consequences (James, 1890, 1950). An intentional action, according to the ideomotor theory, can be triggered simply by anticipating these consequences (action–effect or A–E bindings) (Hommel et al., 2001; Prinz, 1997). Externally guided actions, on the other side, help the agent to adapt his behavior to environmental demands. This type of behavior is based on associations between cueing stimuli and subsequent actions (stimulus–response or S–R bindings).

For a long time, the focus of psychological research was on the exploration of the functional and neural underpinnings of externally guided actions. During the last years, however, research focused increasingly on the exploration of internally guided actions and how they differ from externally guided actions (Cunnington et al., 2002; Jahanshahi et al., 1995; Keller et al., 2006; Waszak et al., 2005; Wiese et al., 2004, 2005). Differences between the two modes of action are observed on the behavioral as well as on the neural level. On the behavioral level, it has been shown that reaction times of externally guided actions are shifted toward the triggering stimuli, whereas reaction times of internally guided actions are shifted towards the produced effects (Keller et al., 2006; Waszak et al., 2005). Similarly, Haggard et al. (2002) found that perceptual onset times of actions and their ensuing effects, on the one hand, and of stimuli and subsequent actions in response to them, on the other hand, attracted each other in time. These findings are in line with the notion that stimuli and responses as well as actions and effects share combined representations (S–R and A–E bindings) (Hommel et al., 2001; Prinz, 1997).

Regarding the underlying neuroanatomical differentiations between the two action modes, Goldberg (1985) emphasized the distinction between a medial and a lateral premotor system, which are involved in internally vs. externally guided actions, respectively.

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However, as Jahanshahi et al. (1995) outlined, even though the concept is very attractive, recent data question the anatomical and functional distinctiveness of major components of the two systems and suggest that their specialization is a matter of degree rather than absolute. This is supported by findings from electrophysiological as well as neuroimaging experiments which suggest that in both action conditions the same areas are activated, but to a stronger degree in the internally guided condition. On the neurophysiological level, there is evidence that the medial wall of the frontal lobe plays a major role in the execution of internally as compared to externally guided actions. According to Picard and Strick (1996), the fronto-median wall consists of the supplementary motor area (SMA), subdivided into the preSMA and the SMA proper, as well as the cingulate motor areas (CMA), which are subdivided into the rostral cingulate zone (RCZ), and the caudal cingulate zone (CCZ).

It is important to note that the decision to perform an internally guided action has at least two components. First, the agent must decide which action out of a certain subset of actions to perform ('what-component'), and he must determine when to perform the action ('when-component'). Most studies that have been published in recent years explored the second component. Usually, in these studies, a condition during which subjects self-initially conducted a key press was compared with a condition in which subjects responded to a visual (Debaere et al., 2003; Deiber et al., 1999; Wiese et al., 2004) or acoustic cue (Cunnington et al., 2002; Jahanshahi et al., 1995; Jenkins et al., 2000). From now on, whenever we refer to the when-component of an action, we will call the action internally or externally *timed*.

However, more recently some studies also dealt with the 'what-component' of voluntary action (Cunnington et al., 2006; Lau et al., 2004a, 2006; van Eimeren et al., 2006). Most of these studies report activation loci in the medial wall of the frontal lobe as a neural correlate of internally guided actions, although the exact locations of activation differ from study to study. While some report peak activation in the preSMA (Deiber et al., 1999; Lau et al., 2006), others show activation in the cingulate motor areas (Debaere et al., 2003; Deiber et al., 1999; Jenkins et al., 2000; Wiese et al., 2004) or in both areas (Cunnington et al., 2006; Deiber et al., 1999; Lau et al., 2004a; van Eimeren et al., 2006). From now on, whenever we refer to the what-component of an action, we will call the action internally or externally *selected*. (We use the term internally or externally *guided* in a neutral manner, whenever *timed* and *selected* are inappropriate.) In the present study, we varied whether an action was internally or externally selected, whereas the timing of the actions was always internally controlled.

On the neuroanatomical level, it is still not clear which role the preSMA and the RCZ play in internally guided actions. One reason for the ambiguity of these findings might be the fact that in most previous studies perceptual and/or motor factors were confounded with the contrast in question (Cunnington et al., 2002; Debaere et al., 2003; Wiese et al., 2005). In some studies, the externally guided condition consisted of a signal that was missing in the internally guided condition (e.g., Cunnington et al., 2002). Thus the two action modes were not directly comparable. Other studies reported only one experimental (internally timed) condition which was compared with a rest condition (Cunnington et al., 2003; Wiese et al., 2005). Therefore activations could not be unequivocally attributed to the internally timed action itself but might have been part of action generation as a whole.

The problem of confounding factors was especially pertinent in this kind of research, because internally and externally guided actions differed in the sensorimotor context in which they took place. A major challenge for the investigation of the neural correlates of internally guided actions is thus, to develop a paradigm in which externally and internally controlled actions differ only in the action mode.

Recently Waszak et al. (2005) conceived a paradigm in which the two modes of action were directly comparable. They studied the electrophysiological signatures of internally and externally selected key presses. In their paradigm, subjects performed a temporal bisection task, making left or right key presses at the midpoint between 35 isochronous pacing signals (a sequence of 'X's presented to the left or the right of the fixation cross). In the internally selected condition, the subjects' key press determined the location of the *subsequent* 'X' on the screen. In this condition, subjects were instructed to generate a random sequence of left and right 'X's. In the externally selected condition, by contrast, the subjects' key press was prompted by the location of the *preceding* stimulus. The movements in a given externally selected run were yoked (in a disguised fashion) to the movements produced in the preceding internally selected run. This paradigm enabled Waszak et al. (2005) to compare movement timing and EEG-correlates of internally and externally selected actions, although the sensorimotor context of the actions and the kinematics and dynamics of the actions were identical in the two conditions. In order to illuminate the neural correlates of internally selected actions, the present experiment used the Waszak paradigm in an fMRI study. Waszaks' (2005) EEG study told us a lot about the timing of the underlying electrophysiological processes of internally selected actions (for details, see Waszak et al., 2005). However, due to the poor spatial resolution of EEG, it could not tell us for sure where the differences in the neural correlates between the two action modes are manifested in the brain. Because we were mainly interested in the yet unsolved question as to which role the preSMA and the RCZ play in internally selected actions, we expected that combining the advantages of Waszak et al.'s paradigm described above with fMRI would help us to shed some light on answering exactly this question.

Material and methods

Subjects

Sixteen healthy subjects (eight males, eight females) with a mean age of 26.33 years (SD ± 2.92) with normal or corrected to normal vision participated in the study. All subjects were right-handed as indicated by scores on the Edinburgh Handedness Inventory (Oldfield, 1971) with a mean laterality quotient higher than 80. Subjects gave written informed consent to the study. All subjects had extensive experience with participating in fMRI studies and had no history of psychiatric, major medical, or neurological disorder. Because of strong movement artifacts, one subject was not included in the analysis.

Stimuli

The stimulus consisted of an 'X' ($1.2° \times 1.2°$ degree of visual angle), which was presented about 2.2° to the left or to the right of a central fixation point. The 'X' was presented in yellow on a black background. Additionally, an auditory pacing-signal composed of sine tones (600 Hz; 100 ms in duration) was presented at the start of a data collection run through the headphones at a loudness level of

95 dBA. As 95 dBA was uncomfortably loud for one subject, the loudness level was reduced to 70 dBA for this person.

Stimulus presentation, synchronization of stimulus presentation, image pulse acquisition, and recordings of motor responses were carried out with the software package Presentation (www.nbs.neuro-bs.com).

Task

The study consisted of two experimental conditions: *I*nternally and *E*xternally selected action conditions that were presented in a blocked order (see Fig. 1). We conducted 20 blocks per condition in an alternating fashion (IEIEIE…). Each block consisted of 35 internally or 35 externally selected actions. A resting phase, lasting about 12,400 ms, followed each block. During this period we showed a blank screen.

In both conditions, the stimuli were presented at a constant inter-stimulus-interval (ISI) of 1200 ms. Each run began with 10 pacing signals, with which participants had to synchronize their key presses. Visual stimuli were presented 600 ms before and 600 ms after the pacing signal, respectively. Afterwards participants continued pressing the keys without the pacing tones, attempting to maintain the target interval as accurately as possible and so as to bisect the interval between two visual stimuli.

In the internally selected condition, subjects could freely choose whether to press the left or the right button and so determined the position of the next stimulus (a left button press was followed by an ‘X’ on the left side of the fixation cross and a right button press was followed by an ‘X’ on the right side of the fixation cross, respectively). In the externally selected condition, subjects reacted with compatible button presses to the preceding stimulus. The S–R mapping was compatible throughout the whole experiment (a left ‘X’ guided a left key press, a right ‘X’ guided a right key press). The sequence of stimuli presented in a given externally selected condition was yoked to the sequence the subject created in the preceding internally selected condition. To prevent subjects from recognizing the sequence, the sequence was presented backwards and the position of the stimuli was vertically mirrored. The whole experiment lasted about 55 min.

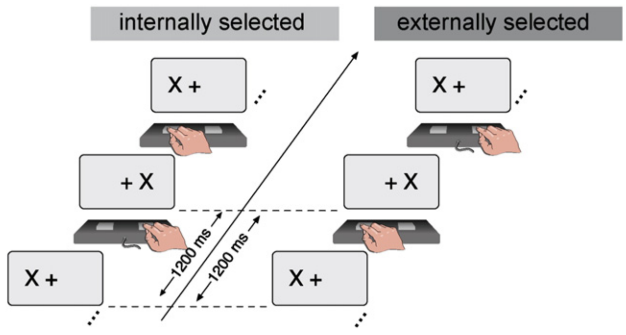

Fig. 1. Paradigm. Illustration of the two conditions. In the internally selected condition, subjects performed left (with the right index finger) or right button presses (with the right middle finger) in order to produce an ‘X’ on the left or right side of a fixation cross. In the externally selected condition, subjects reacted to the stimuli with compatible button presses. Both conditions were identical concerning motor performance, but differed in the action mode in which they were conducted.

fMRI data acquisition

The experiment was carried out on a 3T scanner (Siemens, Erlangen, Germany). Twenty axial slices were acquired (19.2 cm field of view, 64 × 64 matrix, 4 mm thickness, 1 mm gap) parallel to the AC–PC axis and covering the whole brain. Slice gaps were interpolated to generate output data with a spatial resolution of 3 × 3 × 3 mm. A single shot, gradient recalled echo planar imaging (EPI) sequence was used (repetition time 2400 ms, echo time 30 ms, 90° flip-angle, acquisition bandwidth 100 kHz). Prior to functional runs, corresponding 20 anatomical MDEFT slices and 20 EPI-T_1 slices were acquired with the same geometrical parameters (slices, resolution) and the same bandwidth as used for the fMRI data. Stimuli were displayed using VisuaStim (Magnetic Resonance Technologies, Northbridge, USA), consisting of two small TFT-monitors placed directly in front of the eyes, simulating a distance to a normal computer screen of about 100 cm with a resolution of 800 × 600 and a refresh rate of 60 Hz.

fMRI data analysis

Data processing was performed using the software package LIPSIA (Lohmann et al., 2001). This software package contains tools for pre-processing, co-registration, statistical evaluation, and visualization of fMRI data. First, functional data were corrected for motion using a matching metric based on linear correlation. Then, a sinc-interpolation algorithm was applied to correct for the temporal offset between the slices acquired in one scan. Data were filtered with a spatial Gaussian filter with 5.65 mm (sigma = 0.8) full width at half maximum (FWHM). A temporal high-pass filter with a cut-off frequency of 1/160 Hz was used for baseline correction of the signal. All functional data sets were individually registered into stereotaxic Talairach space using participant’s individual high-resolution anatomical images. This 3D reference data set was acquired for each participant during a previous scanning session. The 2D anatomical MDFET slices, geometrically aligned with the functional slices, were used to compute a transformation matrix containing rotational and translational parameter, which registers the anatomical slices with the 3D reference T1 data set. These transformation matrices were normalized to the standard Talairach stereotactic space (Talairach and Tournoux, 1988) by linear scaling and finally applied to the individual functional data. The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1995; Worsley and Friston, 1995). The design matrix was generated with a boxcar function which was convolved with the hemodynamic response function. The two experimental conditions and the resting period were modeled as separate regressors. The model equation, including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley and Friston, 1995). In the following, contrast images were generated for each subject. As noted before, each individual functional data set was aligned with the standard stereotactic reference space, so that a group analysis based on the contrast images could be performed. The single-participant contrast images were then entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample *t*-test across the contrast images of all subjects that indicated whether observed differences between conditions were significantly distinct from zero. Subsequently, *t*-values were transformed into *z*-scores. Results were corrected for multiple comparisons using a combination of individual voxel probability thresholding and minimum cluster-size thresholding (Forman et al., 1995; Xiong et al., 1995). Given an original significance threshold of $z=3.09$ (uncorrected), 1000 iterations of Monte-Carlo simulations were used to confirm that the true false-positive probability of $p<0.001$ corresponds to a minimum cluster size of 1323.00 mm^3.

Furthermore, we were interested in obtaining region∗condition interactions in the signal-strength between a region in the rostral cingulate zone (RCZ) and a region in the preSMA. The RCZ coordinate was derived from the random effects analysis of the contrast between internally and externally selected condition and was centered at a local maximum of the z-map. The preSMA coordinate (2 4 54) was derived from Lau et al. (2004b). As the study of Lau et al. (2004b) used MNI coordinates, we transformed these MNI coordinates to Talairach space using Matthew Bretts' non-linear transformation (http://imaging.mrc-cbu.ac.uk/imaging/MNITalairach).

We defined a mask around each region with a radius of 6 mm. Within each subject and region (Voxel), a mean contrast was calculated separately for each condition. The mean values of the RCZ and preSMA subsequently entered a repeated measures ANOVA with factors condition and region. Effects were considered to be significant at an alpha of 0.05 with a Bonferroni correction for multiple comparisons. In a post hoc analysis, we then calculated differences between the two conditions for each region using two-sided Student's t-tests with effects to be considered significant at an alpha of 0.05.

Analysis of behavioral data

Only action times (time of key press [ms] after onset of the preceding stimulus) within the time window between 250 and 950 were retained for further analysis. Mean action times of the two conditions were compared with a two-tailed t-test. Moreover, for each condition, we ran a t-test against the bisection point (=600 ms).

Results

Behavioral data

T-tests against the bisection point revealed that action times differed in both conditions significantly from 600 ms (internally selected: $t(14)=-3.025$, $p<0.009$; externally selected: $t(14)=-5.440$, $p<0.000$). Furthermore, action times in the internally and externally selected condition differed significantly in the expected direction (MEAN: 569 ms vs. 501 ms; SE: 39.59 ms vs. 70.60 ms), $t(14)=4.238$, $p<0.001$. Mean asynchronies were smaller for the internally selected (−31 ms) than for the externally selected condition (−99 ms) (Fig. 2).

fMRI data

Whole-brain analysis

Internally vs. externally selected actions. As expected, the direct comparison of internally vs. externally selected actions revealed activation in the medial wall of the frontal lobe, namely in the rostral cingulate zone (RCZ). Moreover, we found activations in the lateral prefrontal cortex (lPFC) extending to anterior PFC, in the inferior parietal lobe (IPL), and bilaterally in the insula (Fig. 3) (Table 1). Most importantly, in contrast to previous studies, we found no activity in the preSMA for this contrast. The reverse contrast of externally vs. internally selected actions showed no significant activations. Baseline contrasts are reported in the Supplementary data.

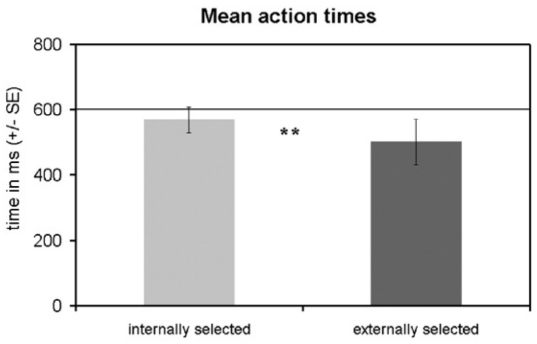

Fig. 2. Behavioral data. Action time (±SE) during internally and externally selected condition. The asterisk indicates significant differences between internally and externally selected actions. The bold line indicates the bisection point.

Signal-strength analysis

Because we were mainly interested in the role of the RCZ and the preSMA in internally selected actions, we ran an ANOVA with the factors region (RCZ and preSMA) and condition (internally vs. externally selected). The analysis revealed a significant region* condition interaction ($F(1,14)=13.706$; $p=0.002$; Fig. 3). As already obvious from the whole-brain analysis, the post hoc analysis revealed significant differences between the internally and externally selected condition only in the RCZ but not the preSMA (preSMA: $t(14)=1.369$, $p=0.193$; RCZ $t(14)=5.053$; $p=0.000$). Thus it seems as if only the RCZ differentiated between internally and externally selected actions. The preSMA showed equal activity in both conditions and thus did not differentiate between internally and externally selected actions.

Discussion

The aim of the current fMRI study was to disentangle the role of the preSMA and the RCZ in internally selected actions without confounding motor and perceptual differences. We employed the paradigm developed by Waszak et al. (2005) in which internally and externally selected actions did not differ as concerns the timing, the sensorimotor context, and the kinematics of the movements. In the direct comparison of internally vs. externally selected actions, a widespread cortical network was found to be activated including frontolateral and inferior parietal brain areas. Most crucially, an activation in the RCZ was observed. A signal-strength analysis showed preSMA and RCZ activation for both internally and externally *selected* actions. However, in contrast to the RCZ, the preSMA did not differentially contribute to internally selected actions.

The behavioral data showed that movements generally preceded the true bisection point (for a discussion of these "negative asynchronies" see for example Aschersleben and Prinz, 1995). More importantly, the results replicated the finding from Waszak et al. (2005; in the behavioral domain) and Haggard et al. (2002) that triggering stimulus and response, on the one hand, and action and ensuing effect, on the other hand, attract each other temporally. This finding suggests that depending on the mode of movement the

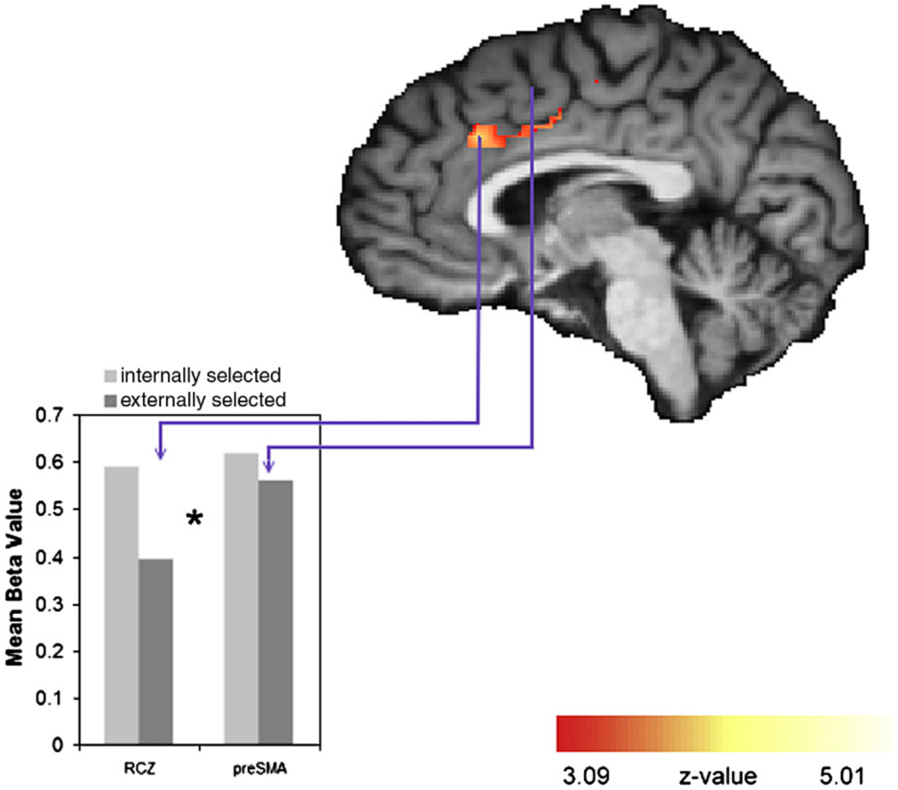

Fig. 3. Contrast between internally and externally selected action. The contrast was averaged over 15 subjects (z-threshold at $z=3.09$, corrected) and mapped to an individual brain from the in-house database. The diagram reports mean beta values for internally and externally selected actions in a region of the RCZ and a region of the preSMA (RCZ Talairach-coordinates: x: 3, y: 23, z: 33 and preSMA MNI-coordinates: x: 2, y: 4, z: 54, Talairach-coordinates: x: 2, y: 6, z: 49). RCZ coordinate is from the contrast internally vs. externally selected actions; preSMA coordinate is from Lau et al. (2004b). The asterisk indicates the significant interaction region * condition.

subjects operate in, sensory-motor integration involves stimuli and responses on one hand or actions and effects on the other hand (see Herwig et al., in press; Waszak et al., 2005).

The role of the RCZ in internally selected actions

As most of the previous studies dealing with internally selected actions, the results of the present study showed that both RCZ and preSMA are involved in internally selected actions. However, when controlling for perceptual and motor confounds, only the RCZ is differentially involved in internally selected as compared to externally selected actions. The preSMA seems to contribute equally to both kinds of actions.

That the RCZ is involved in internally selected actions has been shown in several other fMRI studies (Cunnington et al., 2003, 2006; Debaere et al., 2003; Deiber et al., 1999; Lau et al., 2004a; van Eimeren et al., 2006; Wiese et al., 2004, 2005).

However, the functional role of the RCZ is still under discussion. The RCZ has been associated with a multitude of cognitive control processes, from “higher” cognitive functions to more motor-related functions like relating actions to their effects (Rushworth et al., 2004). In this latter vein, Walton et al. (2004) argue that it is not performance monitoring or reward guided action selection per se that causes RCZ activity but the process of assessing the consequences of a choice made by the subject. This notion nicely fits to the present results. In our study, the subjects’ actions resulted in the presentation of the corresponding stimulus only in the condition with internally selected actions. Along the lines of the ideomotor principle (James, 1890, 1950; Prinz, 1997), we assume that in this condition the action representation is activated by anticipation of the actions’ effect. In the externally selected condition, by contrast, there was no action–effect contingency. In this condition, so our reasoning goes, the action representation is activated by the triggering stimulus. Hence, RCZ activation might be higher in internally selected actions as compared to externally selected

Table 1
Anatomical location and Talairach coordinates with $z>3.09$ ($p=0.001$, corrected)

Anatomical area	Side	$z_{\max}$	Talairach coordinates		
			x	y	z
Frontal					
Rostral cingulate zone	R	4.18	3	23	33
Anterior prefrontal cortex	L	3.53	−18	68	18
Insula	L	4.03	−39	5	6
Insula	R	4.90	39	8	0
Parietal					
Inferior parietal lobe	R	5.00	54	−31	36
Inferior parietal lobe	R	4.35	48	−37	45

Activations with a minimum cluster size of 1323 mm^3 are shown. Comparison internally vs. externally selected actions. The table contains Talairach coordinates (x y z) of the most intense activated voxels of the cluster.

actions, simply because only the former necessitate action–effect anticipation.

Support for this notion comes also from the behavioral domain. Herwig et al. (in press) compared action–effect learning in two conditions similar to the two conditions investigated in the present study. The experiment consisted of an acquisition and a test phase. In the acquisition phase, subjects performed actions that were followed by certain effect tones. Importantly, one group of subjects – the internally selected group – was required to freely select between the two possible actions. In another group – the externally selected group – subjects' actions were determined by external stimulus events. Thus Herwig et al. tested two conditions that probably involve high and low activation of the RCZ, respectively. The results of the test phase showed action–effect learning only for the internally selected acquisition group (for details, see Herwig et al., in press). The results are thus consistent with the idea that RCZ activation is related to effect anticipation (and therefore also with action–effect learning), as supposed by the theoretical framework put forward by Rushworth et al. (2004).

However, there is another possible explanation for the RCZ activation found in the present study. Lau et al. (2004a,b) as well as Cunnington et al. (2005), for example, argue that randomly selecting one out of a set of possible responses constitutes an underdetermined response and therefore triggers response conflict. Monitoring response conflict has repeatedly been related to RCZ activation (Botvinick et al., 2001; Botvinick et al., 2004; Carter et al., 1998; Kerns et al., 2004). Thus the RCZ activation reported above may reflect a sort of conflict monitoring. However, notice that this notion can hardly explain why several studies found RCZ activation when subjects could chose *when* to press a certain *predetermined* button (Cunnington et al., 2003; Deiber et al., 1999; Jenkins et al., 2000; Wiese et al., 2004, 2005). In these studies, there was only one response required and, therefore, no response conflict of the type outlined above.

At any rate, that the RCZ plays a major role in internally selected actions is also supported by neuroanatomical considerations. The RCZ sends efferents both to the primary motor cortex and to the spinal cord, thus having direct influence on motor behavior (Dum and Strick, 1991). Shima and Tanji (1998) suggest that, because of their anatomical connectivity with the preSMA and primary motor cortex, the cingulate motor areas are in a pivotal position to process the information which is necessary to select voluntary actions. Support for this assumption comes from the fact that, in voluntarily timed actions, the cingulate motor areas have been shown to be activated before the preSMA and the primary motor cortex (Ball et al., 1999; Cunnington et al., 2003).

Role of the preSMA

The second main result of this study is that preSMA activation did not differ between internally and externally selected actions. This is to be expected if the role of the preSMA is not linked to the selection of the action, but rather to its timing or initiation. Notice that in both conditions we investigated if subjects had to time the action such as to meet the bisection point. Accordingly, whether externally or internally *selected*, the trigger to initiate the action is necessary in both conditions to the same degree, such that preSMA activation was bound to be the same in both conditions.

This idea is in line with previous studies that associate the preSMA to the generation of self-initiated and self-paced (internally timed) actions (Cunnington et al., 2002, 2003; Debaere et al., 2003; Deiber et al., 1999; Wiese et al., 2004). Likewise, bilateral lesions impaired the ability to generate simple internally timed actions (Thaler et al., 1995). More recently, Cunnington et al. (2006) suggested that the preSMA plays a major role in maintaining responses in readiness for action.

To sum up, our findings are thus compatible with the view that the RCZ activation is more closely linked to internally selected actions ('what-component'), whereas the preSMA might be more closely linked to the internal timing of an action ('when-component'), i.e., to find the right moment for the action. This latter point has already been suggested more than 20 years ago by Kornhuber and Deecke who hypothesized in the commentary to Goldberg's article (1985) (p. 591):

> Because of this functional uniqueness a motivational role with emphasis on the will has been ascribed to the SMA (Kornhuber, 1980). However, motivation is a complex function with several independent subfunctions concerning *what* to do, *how* to do it and *when* to start. The latter function that of finding the right moment for action, is in our view the task of the SMA (Kornhuber, 1984).

Activations due to working memory and attentional load

Lateral and anterior PFC

Besides activation in the medial frontal wall, we observed significant activation differences between the two action conditions which were located in the right lPFC, extending to the anterior PFC. Even though these activations were not in the focus of our interpretations about the neural bases of internally selected actions, we have some clear ideas about their function. One possible explanation for the lPFC activation might be working memory processes due to the generation of random button presses (Jahanshahi et al., 1998). Another possible explanation for the lPFC activation in our study is that it reflects stronger attentional demands during internally selected actions (Lau et al., 2004a).

Another detail worthwhile to be reported is that, in contrast to previous imaging studies, the lPFC activation we found reaches up to the anterior PFC (BA 10). This activation might be due to branching processes. According to Koechlin et al. (1999), branching is the ability to keep in mind primary goals while exploring and processing secondary goals. Related to our study, this would mean that while our subjects had to bisect the task with left or right button press, they should randomize their button presses and thus hold in mind which buttons they pressed before.

IPL

As several previous fMRI studies, we found for internally selected actions a stronger bilateral activation in the inferior parietal lobe (BA 40) (Ball et al., 1999; Jahanshahi et al., 1995; Jenkins et al., 2000; Wiese et al., 2005). This area is reciprocally connected to the lPFC (Cavada and Goldman-Rakic, 1989), which, as outlined above, was also strongly activated during the internally selected action condition. Hence, we suggest that the parietal activation also reflects stronger attentional demand due to the random number generation.

To conclude, given the obvious requirement of generating random sequences in the internally but not the externally selected condition, we found a nice dissociation in the fMRI data between areas that are primarily involved in the generation of random sequences (lPFC activations) and activations associated primarily with internally selected actions (activations in the medial frontal wall).

Conclusion

The present fMRI study aimed at investigating the neural correlates of internally selected actions. For this purpose, we compared internally and externally selected actions within a paradigm in which both conditions differed only in the action mode in which they were conducted. The behavioral as well as the functional imaging findings are in general agreement with previous studies that – compared to the current study – were less strictly controlled and therefore confounded by perceptual and motorical differences. We were able to show, first, that the preSMA contributes to both internally and externally selected actions in a similar way and, second, that the RCZ is differentially activated in internally as compared to externally selected actions. We suggest a primary role for the RCZ in the internal selection of actions (‘what-component’), whereas the preSMA might be more closely linked to the internal timing of an action (‘when-component’), i.e., to find the right moment for the action. Activations in the lPFC and IPL that were also found during internally selected actions possibly reflect working memory and attention-related processes due to the random generation of button presses as well as due to higher attentional load in the internally selected condition.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.06.018.

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