Neuroscience 259 (2014) 164–171

NEURAL CORRELATES OF IDEOMOTOR EFFECT ANTICIPATIONS

R. PFISTER, [a,b*†] **T. MELCHER,** [a,c†] **A. KIESEL,** [b] **P. DECHENT** [d] **AND O. GRUBER** [a]

[a] *Centre for Translational Research in Systems Neuroscience and Clinical Psychiatry, Department of Psychiatry and Psychotherapy, Georg-August-University, 37075 Goettingen, Germany*

[b] *Department of Cognitive Psychology, University of Wuerzburg, 97070 Wuerzburg, Germany*

[c] *Center of Old Age Psychiatry, Psychiatric University Hospital, Basel, Switzerland*

[d] *University Medical Center Goettingen, MR-Research in Neurology and Psychiatry, Georg-August-University, 37075 Goettingen, Germany*

Abstract—How does our mind produce physical, goal-directed action of our body? For about 200 years, philosophers and psychologists hypothesized the transformation from mind to body to rely on the anticipation of an action's sensory consequences. Whereas this hypothesis received tremendous support from behavioral experiments, the neural underpinnings of action control via such ideomotor effect anticipations are virtually unknown. Using functional magnetic resonance imaging, the present study identified the inferior parietal cortex and the parahippocampal gyrus as key regions for this type of action control – setting the stage for a neuroscientific framework for explaining action control by ideomotor effect anticipations and thus enabling a synthesis of psychological and neuroscientific approaches to human action. **© 2013 IBRO. Published by Elsevier Ltd. All rights reserved.**

Key words: action effects, ideomotor theory, action control, sensory anticipations.

INTRODUCTION

The anticipation of desired outcomes is an integral part of goal-directed behavior. These outcomes, i.e., action effects, even seem to fulfill a central and possibly indispensable function in action control. This role is most prominently expressed in ideomotor theory (Herbart, 1825; cf. Hommel et al., 2001; Kunde, 2001; Shin et al., 2010): Sensory effect anticipations lead to a backward activation of motor commands which have produced the respective sensory codes before. In other words, voluntary actions can be addressed in terms of sensory anticipations.

In behavioral science, this functional role of effect anticipations is well documented by experiments in the response–effect (R–E) compatibility paradigm (Kunde, 2001; cf. also Kunde et al., 2004; Rieger, 2007; Pfister et al., 2010; Hubbard et al., 2011; Badets et al., 2013; Pfister and Kunde, 2013). The critical experimental variation in these studies concerns the relation between performed motor actions and contingently following sensory action effects. In spatial R–E compatibility, for instance, key presses with the left hand produce left visual action effects in some trials (*compatible condition*) whereas they produce right visual action effects in other trials (*incompatible condition*). Reaction times (RTs) are typically faster in the compatible condition than in the incompatible condition, even though the effects are not present before action execution (Kunde, 2001). The R–E compatibility effect thus clearly indicates that action effects are *anticipated* before action execution and play a functional role in the selection and initiation of voluntary actions.

From a functional perspective, it is important to distinguish between *environment-related* action effects, such as the effects used in R–E compatibility designs, and *body-related* action effects such as proprioceptive or kinesthetic effects (Janczyk et al., 2009; Pfister and Kunde, 2013; Pfister et al., 2013b). Whereas body-related action effects are tightly bound to the action, recent studies demonstrated that environment-related action effects seem to be flexibly in- or excluded from action control (Pfister et al., 2010; Gaschler and Nattkemper, 2012). An important determinant for the inclusion of environment-related effects into action control seems to be whether actions are selected endogenously or exogenously: Action control by the anticipation of environment-related action effects tends to more pronounced for endogenously selected actions (i.e., free action choices) as compared to exogenously selected actions (i.e., forced-choice responses; see Herwig et al., 2007; Herwig and Waszak, 2012). This conclusion seems to hold true especially for situations in which action–effect relations are highly variable and depend on the current context (Pfister et al., 2010). By contrast, stable action–effect relations are exploited by both, endogenously and exogenously selected actions (Pfister et al., 2011; Wolfensteller and Ruge, 2011; Pfister and Kunde, 2013; for an additional moderating role of deliberate intentions, see Ansorge, 2002; Zwosta et al., 2013).

*Correspondence to: R. Pfister, Department of Cognitive Psychology, University of Wuerzburg, Röntgenring 11, 97070 Wuerzburg, Germany. Tel: +49-(0)931-3181363; fax: +49-(0)931-3182815.
E-mail address: roland.pfister@psychologie.uni-wuerzburg.de (R. Pfister).
† These authors contributed equally to the present work.

Abbreviations: ANOVA, analysis of variance; fMRI, functional magnetic resonance imaging; RT, reaction time.

0306-4522/13 $36.00 © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neuroscience.2013.11.061

Before effect anticipations can be used for action control, agents need to acquire associations between actions and following effects. More precisely, ideomotor theory assumes these associations to be bidirectional (Elsner and Hommel, 2001; Hoffmann et al., 2009). Such bidirectional associations are typically probed for by experimental designs that employ a learning phase and a following test phase. In the learning phase, actions contingently produce specific effects. In the test phase, these former action effects are presented as imperative stimuli, assuming that the former effects would prime the associated responses. Reliable priming effects were indeed found in a variety of settings (for a review, see Shin et al., 2010). Moreover, such priming paradigms have been successfully used to study the neural basis of action–effect associations by contrasting the neural consequences of presenting former action effects as stimuli during simple RT tasks (Elsner et al., 2002; Melcher et al., 2008, 2013; Kühn et al., 2010, 2011; Ruge et al., 2010). These studies highlighted the hippocampus and the (pre-)supplementary motor area (SMA) as critical structures mediating response priming by former effect stimuli.

Despite the rich behavioral evidence and first neuroscientific studies on the acquisition of bidirectional action–effect associations, action control via ideomotor effect *anticipations* is not well understood on the neural level. In order to gather direct evidence for the neurophysiological basis of this process, we adopted a modified version of the R–E compatibility paradigm (Pfister et al., 2010) and optimized it for event-related functional magnetic resonance imaging (fMRI): Participants pressed a left or right response key to produce spatially compatible, neutral, or incompatible action effects. These arbitrary action effects were blue squares appearing at different locations, depending on the current mapping of responses and effects. In order to perform event-related fMRI scanning, the R–E mapping varied on a trial-to-trial basis with the current mapping being cued at the beginning of each trial (Fig. 1; design adopted from Pfister et al., 2010). In most trials (67%), participants were instructed which key to press (exogenous selection) whereas they could freely choose between both response alternatives in the remainder of the trials (endogenous selection). The higher frequency of exogenous selection as compared to endogenous selection was designed to induce conditions with equally strong sensory and motor activity but – crucially – varying proportions of effect anticipations due to contextualized action–effect relations (Pfister et al., 2010). Consequently, our analyses exploited the contrast of endogenously and exogenously selected actions to probe for the signature of effect anticipations by means of regression analyses. The general rationale of this analysis was that the regions mediating action control by effect anticipations would exhibit a pattern of activity that gradually varies with the observed behavioral effects.

Given the sensory nature of action–effect anticipations (Kunde, 2001; Kunde et al., 2004), we expected the sensorimotor integration of environment-related, visuo-spatial action effects to result in increased activity of the parietal cortex (Wolpert et al., 1998; Fogassi et al., 2005) whereas motor cortices should not be differentially involved (see above). Furthermore, we expected additional activity in the hippocampal system due to retrieval of spatial action–effect knowledge (Hayes et al., 2004).

EXPERIMENTAL PROCEDURES

Participants and apparatus

Eighteen healthy volunteers from the University of Göttingen (seven males, all right-handed) were paid for participation. The mean age was 23.72 years (SD = 2.62), participants reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment. The study was approved by the local ethics committee and participants signed an informed consent form prior to participation.

The employed paradigm is derived from previous behavioral experiments on R–E compatibility with trial-to-trial variations of R–E relations (Fig. 1; see Pfister et al., 2010). Cue boxes, presented in white, and effect squares, presented in blue or orange, measured 2.5 × 2.5 cm. The cues indicating neutral trials were shown in the center of the screen (vertically aligned) whereas cues for compatible and incompatible trials were shown in the upper or lower half of the screen (horizontally aligned). The mapping of cue positions (high vs. low) to compatibility conditions (compatible vs. incompatible) was counterbalanced across participants: Cue boxes in the upper half indicated compatible trials for one half of the participants and incompatible trials for the other half. Target stimuli were displayed in 24 point Arial font. We used left- and right-pointing arrows (0.5 × 0.6 cm) to signal forced-choice responses, i.e., exogenous selection, and exclamation marks (0.1 × 0.6 cm) to signal free response choices, i.e., endogenous selection.

Procedure

Each trial started with a 1000-ms presentation of two cue boxes that indicated the current R–E relation (incompatible vs. neutral vs. compatible). The target stimulus appeared after a variable inter-stimulus-interval of either 500, 1000, or 1500 ms. It stayed on screen for 200 ms and participants had a time window of 1000 ms to respond. Correct responses triggered a 500-ms presentation of a blue effect square in 90% of the trials whereby the location of the square depended on the current compatibility condition. Thus, in compatible trials, the effect square was presented on the same side as the key pressed whereas in incompatible trials, the effect square was presented on the opposite side. In neutral trials, the square was presented randomly either in the top or bottom center. As in previous experiments (Pfister et al., 2010), 10% of the trials featured a deviant effect, i.e., the effect was an orange instead of a blue square. These deviant effects were included to draw participants' attention to the action effects. Participants

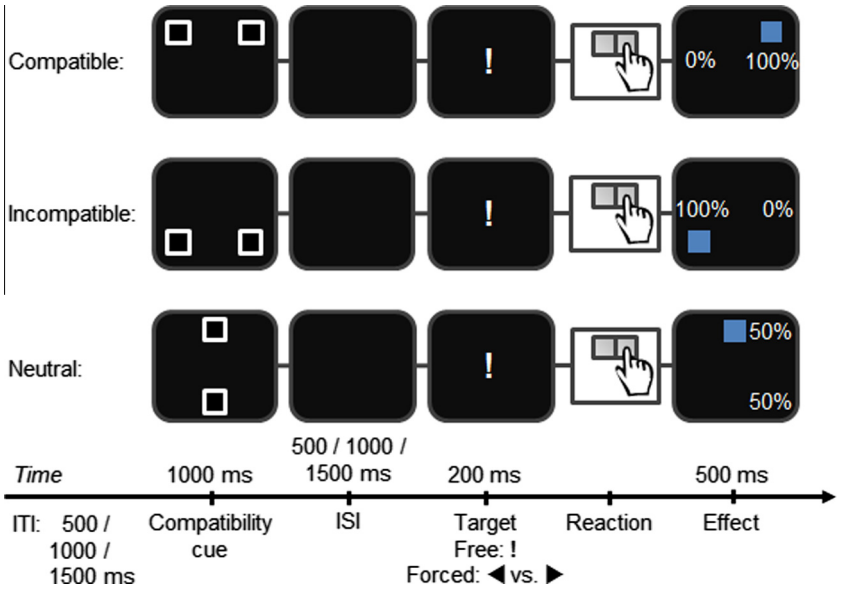

Fig. 1. Trial procedure. Following a variable oversampling interval (500, 1000, or 1500 ms), a cue indicated the mapping of left and right response keys and spatial position of action effects (left, central, right), creating compatible, neutral, and incompatible action–effect mappings. After a jittering interval (500, 1000, or 1500 ms), a free or forced choice target stimulus (endogenous vs. exogenous selection) instructed the participants to perform a key press that triggered a blue square on the computer screen. The location of the square (left, central, or right) depended on the cued compatibility relation and the performed action.

had to react to deviant effects by pressing both keys simultaneously and these trials were excluded from all RT and fMRI analyses. Furthermore, trials with responses prior to the target stimulus or RT < 100 ms (0.1%), response omissions (0.2%), wrong key presses in forced choice trials (1.6%), and key presses in reaction to normal effects (0.03%) were excluded from data analysis (2.0% in total).

Participants completed four blocks of 63 trials outside the scanner as training. In this training session, they first experienced each compatibility condition in a separate block and continued with one block of mixed compatibility conditions. The following scanning session consisted of three runs of 126 trials each. In compatible trials, responses produced an action effect on the same side of the display whereas the action effect appeared centrally in neutral trials and on the opposite side in incompatible trials. The three imperative stimuli appeared equally often throughout the experiment, equating to a proportion of 33% free choice targets (endogenous selection). The propotion of 33% free choice targets (as compared to 50% in Pfister et al., 2010) was used to prevent carry-over effects of endogenous on exogenous selection; the effectivity of this manipulation had been validated a behavioral pilot study.

Data acquisition

The scanning session started with a high-resolution structural scan of each participant (three-dimensional magnetization-prepared rapid-acquisition gradient echo; MP-RAGE), using a 3T Siemens Trio tomograph. The following functional images comprised thirty-three axial slices of the brain ($3 \times 3 \times 3\ mm^3$, 20% gap), recorded in ascending order parallel to the AC–PC plane. A gradient-echo echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, flip angle: 70°, field of view: 192 mm) produced a total of 1143 volumes over the course of the three runs. Four initial dummy volumes were discarded from each session to allow for T1 equilibration effects.

Statistical analysis

Functional images were preprocessed and analyzed with SPM8 (Wellcome Trust Centre for Neuroimaging, University College London, London, UK). Preprocessing comprised coregistration, correction for movement-related artifacts (realignment and unwarping), corrections for slice-time acquisition differences and low-frequency fluctuations, normalization into standard stereotactic space (MNI template, Montreal Neurological Institute, Canada), and spatial smoothing with an isotropic Gaussian kernel filter at 9 mm full-width at half-maximum (FWHM).

Statistical analyses relied on the general linear model approach of SPM. A vector of temporal onsets for each experimental condition was convolved with a canonical hemodynamic response function to produce a predicted hemodynamic response to this condition. The to-be-modeled conditions resulted from the orthogonal combination of the factors compatibility (incompatible vs. neutral vs. compatible), selection mode (endogenous vs. exogenous) and response (left vs. right). Trials with deviant effects or errors were modeled separately but were not included in further analyses.

For RT distribution analysis, we corrected for outliers by excluding individual trials with RTs that deviated more than 2.5 standard deviations from the respective

mean, calculated separately for each participant and design cell. To avoid violations of sphericity, we used multivariate tests for all reported analysis of variance (ANOVA) statistics; for an optimal comparison with the fMRI analysis, all remaining behavioral analyses were conducted without outlier correction.

RESULTS

Behavioral R–E compatibility effects

Fig. 2 shows the mean RTs in the six conditions of the present experiment. A 2 × 3 repeated-measures ANOVA with the factors compatibility (incompatible vs. neutral vs. compatible) and selection mode (endogenous vs. exogenous) revealed a significant main effect of compatibility, $F(2, 16) = 12.58$, $p < .001$, $\eta_p^2 = 0.61$, and a significant main effect of selection mode, $F(1, 17) = 142.36$, $p < .001$, $\eta_p^2 = 0.89$. Furthermore, a significant interaction, $F(2, 16) = 3.74$, $p = .047$, $\eta_p^2 = 0.32$, indicated a stronger compatibility effect ($RT_{incompatible} - RT_{compatible}$) for endogenously than for exogenously selected actions (19 ms vs. 4 ms). This interaction was qualified by a direct comparison of both compatibility effects, $t(17) = 2.16$, $p_{1\text{-tailed}} = .022$, $d = 0.72$. In other words, even though the action effects were *not* present before action execution, R–E compatibility nevertheless exerted a reliable influence – and this influence was more pronounced for endogenously than for exogenously selected actions.

To ensure that the critical difference in R–E compatibility effects for endogenously and exogenously selected actions did not result from differences in basic RT level (Kunde, 2001), we performed a detailed distribution analysis of the RT data (Fig. 3). To this end, we computed separate means for the distribution quintiles of each combination of the factors choice and compatibility. A 2 × 3 × 5 repeated-measures ANOVA with the factors compatibility, selection mode, and distribution quintile showed all three main effects to be significant (all $ps < .002$, all $\eta_p^2 > 0.52$). Importantly, the interaction of compatibility and selection mode was also significant, $F(2, 17) = 4.53$, $p = .026$, $\eta_p^2 = 0.35$, and this interaction was equally strong across distribution quintiles ($F < 1$ for the three-way interaction). Accordingly, an R–E compatibility effect ($RT_{incompatible} - RT_{compatible}$) emerged already for the first distribution quintile of endogenously selected actions, $t(17) = 3.16$, $p_{1\text{-tailed}} = .003$, $d = 0.74$, whereas R–E compatibility did not approach significance even for the slowest quintile of exogenously selected actions, $t(17) = 0.92$, $p_{1\text{-tailed}} = .185$, $d = 0.22$. The assumed differential role of environment-related effect anticipations for endogenously and exogenously selected actions was thus reliable for the entire spectrum of endogenous and exogenous responses. Additionally, the two-way interaction of compatibility and distribution quintile was not significant ($F < 1$) whereas a significant interaction of selection mode and distribution quintile $F(4, 15) = 14.08$, $p < .001$, $\eta_p^2 = 0.79$, was driven by larger differences between exogenously and endogenously selected actions for slower RTs. Tested individually for each quintile, the RT difference between endogenously and exogenously selected actions was, however, highly significant from the first quintile, $t(17) = 8.12$, $p_{1\text{-tailed}} < .001$, $d = 1.91$, through the last quintile, $t(17) = 8.99$, $p_{1\text{-tailed}} < .001$, $d = 2.12$.

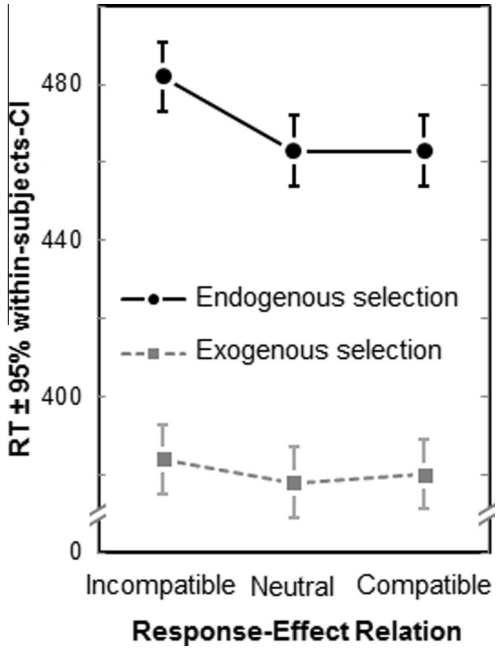

Fig. 2. Main results of the RT analysis. An R–E compatibility effect was present for endogenously selected actions but not for exogenously selected actions, preparing the ground for the corresponding fMRI analysis.

The neural correlates of ideomotor effect anticipations

The analysis of the fMRI data consisted of two separate steps and relied on the differential recruitment of effect anticipations for endogenously and exogenously selected actions as demonstrated by the behavioral results. In the first step, we identified the regions subserving endogenous action control by a simple contrast of endogenously vs. exogenously selected actions. Due to the differential contribution of effect anticipations as demonstrated by the behavioral results, this contrast should include some regions that were responsible for processing ideomotor effect anticipations. Essentially, this first step served as manipulation check in comparison to previous studies on endogenous vs. exogenous actions (Jahanshahi et al., 1995; Pesaran et al., 2008; Rowe et al., 2010; for a historical perspective on this contrast, see Pfister et al., 2012). In the second step, individual behavioral R–E compatibility effects for endogenously selected actions were used as regressors in the above contrast. As the R–E compatibility effect provides a pure measure of action control via ideomotor effect anticipations (Kunde, 2001), it should only correlate with activity in those areas that are involved in ideomotor processes.

The first step (i.e., the contrast of endogenous vs. exogenous selection) identified a pronounced fronto-parietal network that was repeatedly reported for

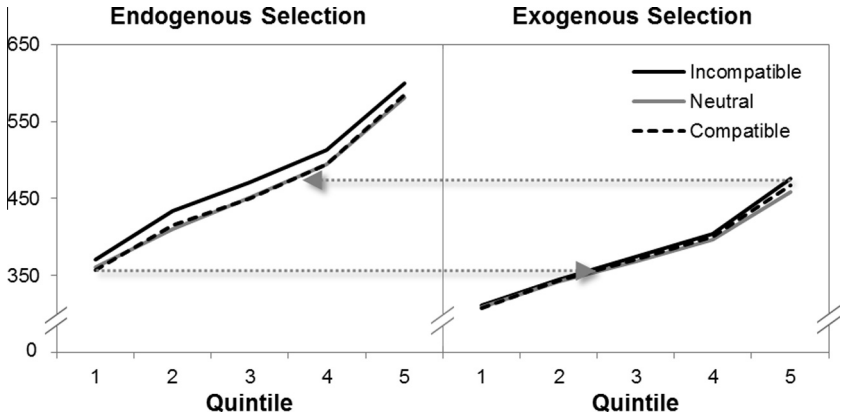

Fig. 3. Distribution analysis of the RT data. An R–E compatibility effect emerged already for the fastest endogenously selected actions whereas the effect was absent for the entire distribution of exogenously selected actions. The more pronounced R–E compatibility effect for endogenously selected actions is thus not caused by the overall longer RTs in this condition but does indeed reflect functional differences.

endogenous action control (Jahanshahi et al., 1995; Karch et al., 2010; Rowe et al., 2010). This network included the rostral cingulate zone, lateral prefrontal areas, insular cortex as well as large parts of parietal cortex (Fig. 4a, see Table 1 for a detailed list of activations).

The following regression analysis identified five circumscribed regions for which activity correlated with behavioral R–E compatibility effects: The left inferior parietal gyrus, the right temporo-parietal junction, the right parahippocampal gyrus as well as left medial and superior frontal gyrus. The lateralized pattern of activity was present for both, left and right hand actions as qualified by separate VOI-based analyses (Table 2).

The neural correlates of the R–E compatibility effect

Additional correlation analyses examined the neurophysiological basis of the R–E compatibility effect itself by using the behavioral compatibility effects as regressor in the contrast endogenous/*incompatible* > endogenous/*compatible*. These analyses mainly yielded significant correlations for sensory association areas in parietal and extrastriate occipital cortices, most prominently the bilateral precuneus and the bilateral lingual gyrus (see Fig. 5; Table 3).

DISCUSSION

The present study investigated the neurophysiological foundation of action control via ideomotor effect anticipations, i.e., the processes that transform anticipated, subjective goals into overt motor behavior. To this end, we employed an R–E compatibility paradigm while performing event-related fMRI. We then used individual R–E compatibility effects as regressors to identify the brain areas that are involved in this type of action control. Given that the behavioral R–E

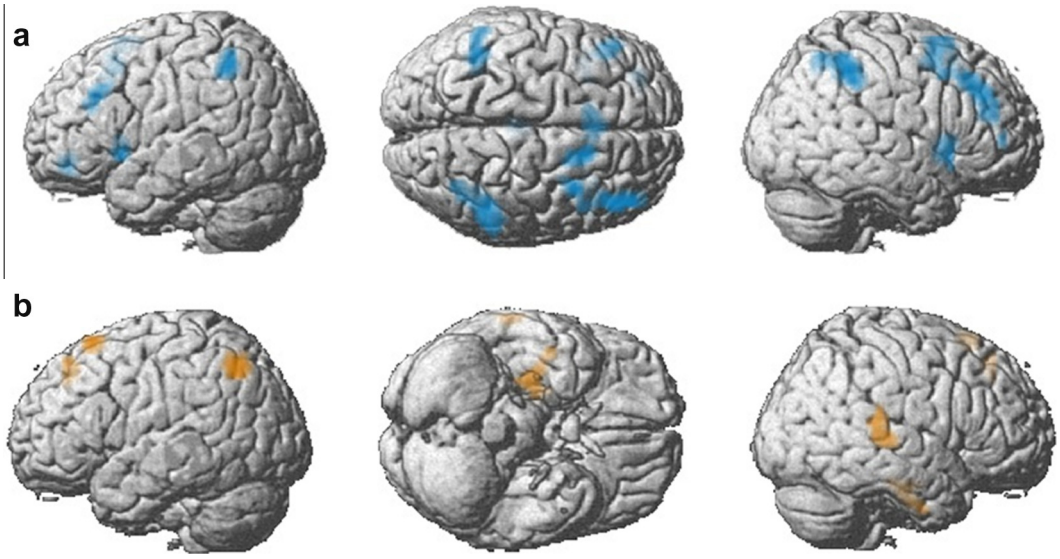

Fig. 4. (a) Fronto-parietal network subserving the control of endogenously selected actions (contrast: endogenous > exogenous selection), thresholded at $p < .050$, FWE-corrected, and a minimum cluster size of $k = 20$ contiguous voxels. See Table 1 for a detailed list of activation foci. (b) Correlation of behavioral R–E-compatibility effects with the signal strength in the main contrast, thresholded at $p < .005$, uncorrected, with a minimum cluster size of $k = 20$ voxels. See Table 2 for a detailed list of activation foci.

Table 1. Activation foci of the contrast ''endogenous vs. exogenous selection''. Anatomical location, cluster size, MNI-coordinates, and peak statistics for the contrast endogenous > exogenous, thresholded at $p < .050$, FWE-corrected, with a minimum cluster size of $k = 20$ voxels. The two columns labeled with 'z' refer to the z-coordinate in MNI space (3rd column from the right) and the test statistic z (right-most column), respectively

Region	BA	Hemisphere	*k*	*x*	*y*	*z*	*t*	*z*
Orbitofrontal	11	L	18	−30	44	−8	9.15	5.43
MFG/DLPFC	9	L	20	−45	29	31	8.09	5.11
MFG/DLPFC	9	R	80	45	35	34	10.01	5.66
	8			42	26	43	9.65	5.57
	46			45	41	22	8.61	5.28
SFG/SMA	6	R	42	18	11	64	10.88	5.87
FEF	6	R	25	36	8	52	9.96	5.65
RCZ	8	L	45	−9	17	52	8.8	5.33
				0	20	46	8.41	5.22
Insula	13	L	24	−36	14	−2	8.31	5.18
Insula	13	R	53	36	11	−2	8.28	5.18
				33	17	4	7.43	4.9
IPG	40	L	37	−42	−49	52	8.28	5.18
				−57	−49	49	7.86	5.04
IPG	40	R	79	48	−43	46	9.18	5.44

BA, Brodmann area; MFG, medial frontal gyrus; DLPFC, dorsolateral prefrontal cortex; SFG, superior frontal gyrus; SMA, supplementary motor area; FEF, frontal eye field; RCZ, rostral cingulate zone; IPG, inferior parietal gyrus.

Table 2. Anatomical location, cluster size, MNI-coordinates, and peak statistics for the regression analysis with behavioral R–E-compatibility effects (contrast: endogenous > exogenous selection), thresholded at $p < .005$, uncorrected, with a minimum cluster size of $k = 20$ contiguous voxels. The two columns labeled with 'z' refer to the z-coordinate in MNI space (3rd column from the right) and the test statistic z (right-most column), respectively

Region	BA	Hemisphere	*k*	*x*	*y*	*z*	*t*	*z*
SFG	6	L	35	−15	23	61	4.85	3.75 *
MFG	8	L	41	−9	35	46	4.26	3.43 *
IPG	40	L	50	−48	−64	46	4.42	3.52 *
Parahippoc.	36	R	53	36	−13	−32	4.20	3.40 *
				30	−22	−23	4.11	3.35 *
				45	−7	−38	3.75	3.13
TPJ/STG	22	R	44	69	−28	4	3.90	3.22 *

BA, Brodmann area; SFG, superior frontal gyurs; MFG, medial frontal gyrus; IPG, inferior parietal gyrus; Parahippoc., parahippocampal gyrus; TPJ, temporo-parietal junction; STG, superior temporal gyrus.

* Significant for each individual hand (contrast: endogenous/left vs. exogenous/left and endogenous/right vs. exogenous/right) as qualified by a correlation of behavioral R–E compatibility effects and the signal change in a VOI ($r = 10$ mm) around the peak voxel of the original regression analysis.

compatibility effect provides a pure measure of ideomotor effect anticipations (Kunde, 2001), the enhanced activity of these regions can only be attributed to processes that relay sensory anticipations to the motor system.

In line with recent neuropsychological studies (Wolpert et al., 1998; Sirigu et al., 2004; Desmurget et al., 2009; Goldenberg, 2009), the present results suggest an important role of parietal circuits for the selection and initiation of actions, especially for action control via anticipated distal action effects. As predicted and outlined above, parahippocampal activity is most likely driven by the retrieval of (spatial) action–effect knowledge (Hayes et al., 2004). Activity in the right temporo-parietal junction, by contrast, might control attentional shifts to the expected location of the upcoming action effects (Karnath et al., 2001) or an evaluation of sense of agency (Spengler et al., 2009).

These results are the first neurophysiological evidence for the brain regions involved in the transformation of anticipated action effects into overt action. The suggested prominent role of the inferior parietal cortex is consistent with recent accounts of parietal function (Sirigu et al., 2004; Fogassi et al., 2005; Goldenberg, 2009; see Melcher et al., 2013, for a role of a related part of inferior parietal cortex – the angular gyrus – for ideomotor learning). For instance, the inferior parietal cortex has been shown to be directly related to the generation of motor intentions in a direct cortical stimulation study (Desmurget et al., 2009). Furthermore, the inferior parietal cortex was identified as a key structure for the understanding of action goals in the mirror neuron framework (Rizzolatti and Matelli, 2003; Rizzolatti and Craighero, 2004; Fogassi et al., 2005). The pronounced effect for inferior parietal circuits, in combination with the limited activity in the superior parietal cortex, also informs the theoretical concept of action control via sensory anticipations (Kunde, 2001; Pfister et al., 2013a). Instead of a direct translation of anticipated sensory effects to motor areas (e.g., Hommel et al., 2001), the present results suggest that sensory anticipations are first relayed to higher centers, most possibly mapping anticipated sensory events in the environment to a multisensory representation (Fogassi et al., 2005). The exact

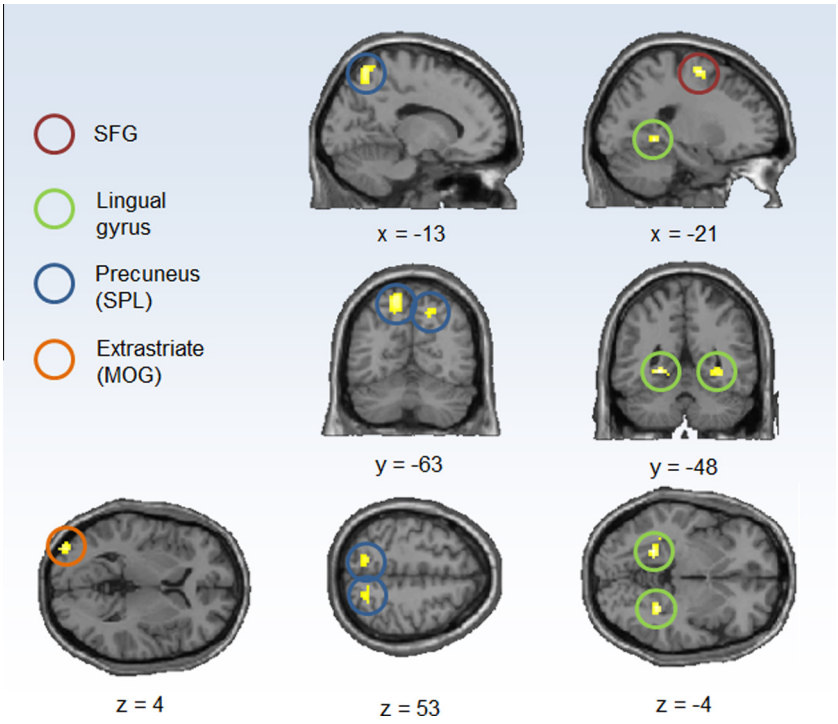

Fig. 5. Correlation of behavioral R–E-compatibility effects with the signal strength in the contrast endogenous/*incompatible* > endogenous/*compatible*, thresholded at $p < .005$, uncorrected, with a minimum cluster size of $k = 20$ voxels. See Table 3 for a detailed list of activation foci.

Table 3. Anatomical location, cluster size, MNI-coordinates, and peak statistics for the regression analysis of behavioral R–E-compatibility effects within the contrast endogenous/incompatible > endogenous/compatible, thresholded at $p < .005$, uncorrected, with a minimum cluster size of $k = 20$ contiguous voxels. All regions listed below show increased effects in the mentioned contrast with an increasing behavioral R–E compatibility effect. The two columns labeled with 'z' refer to the z-coordinate in MNI space (3rd column from the right) and the test statistic z (right-most column), respectively

Region	BA	Hemisphere	*k*	*x*	*y*	*z*	*t*	*z*
SFG	6	L	30	−21	−4	61	4.42	3.52
SPL	7	L	72	−15	−64	61	3.92	3.23
		R	29	19	−81	49	3.52	2.99
Lingual	19	L	20	−24	−49	−5	4.34	3.48
Gyrus				−33	−46	−8	3.11	2.71
		R	36	33	−46	−8	4.18	3.39
MOG	19	L	22	−36	−91	4	3.73	3.12

BA, Brodmann area; SFG, superior frontal gyrus; SPL, superior parietal lobule (precuneus); MOG, middle occipital gyrus (extrastriate cortex).

mechanisms underlying this mapping are an important question for future research that will inform both, psychological and neuroscientific models of human action control (Wolpert et al., 1995; Wolpert and Ghahramani, 2000; Hommel et al., 2001; Haggard, 2008).

Also in line with classical assumptions about the sensory nature of ideomotor effect anticipations (Kunde, 2001) and recent neuroimaging studies (Kühn et al., 2010, 2011), the analyses of the R–E compatibility effect itself revealed sensory association areas in parietal and extrastriate occipital cortices. Interestingly, even though R–E compatibility phenomena are often referred to as measures of conflict due to non-matching anticipations (Kunde, 2001; Pfister et al., 2013a), the present analysis did not show any areas that are commonly associated with conflict processing, such as the anterior cingulate cortex (Botvinick et al., 1999; Gehring and Knight, 2000; Kerns et al., 2004), suggesting that the behavioral R–E compatibility effect is not necessarily a measure of response conflict.

It should also be noted that the present operationalization of action effects differs in a critical aspect from most anticipated action effects in everyday action control. Whereas we focused on rather uninformative and irrelevant action effects (blue squares appearing at a certain location), most actions are certainly performed to trigger more meaningful changes in the environment. Our results are thus likely to represent a rather conservative measure of effect anticipations. In turn, by adopting this conservative perspective on action effects, the present study prepares the ground for a neurophysiological foundation of action control via sensory anticipations. This foundation, however, can only be achieved through a clearer understanding of fronto-parietal interactions in action control as well as the neurophysiological dynamics of ideomotor processes, i.e., an ultimate integration of ideomotor theory as a genuinely psychological concept and classical neurophysiological models of action control.

REFERENCES

Ansorge A (2002) Spatial intention–response compatibility. Acta Psychol 109:285–299.

Badets A, Koch I, Toussaint L (2013) Role of an ideomotor mechanism in number processing. Exp Psyhol 60:34–43.
Botvinick M, Nystrom LE, Fissell K, Carter CS, Cohen JD (1999) Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402:179–181.
Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A (2009) Movement intention after parietal cortex stimulation in humans. Science 324:811–813.
Elsner B, Hommel B (2001) Effect anticipation and action control. J Exp Psychol 27:229–240.
Elsner B, Hommel B, Mentschel C, Drzezga A, Prinz W, Conrad B, Siebner H (2002) Linking actions and their perceivable consequences in the human brain. NeuroImage 17:364–372.
Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G (2005) Parietal lobe: from action organization to intention understanding. Science 308:662–667.
Gaschler R, Nattkemper D (2012) Instructed task demands and utilization of action effect anticipation. Front Psychol 3:578.
Gehring WJ, Knight RT (2000) Prefrontal–cingulate interactions in action monitoring. Nat Neurosci 3:516–520.
Goldenberg G (2009) Apraxia and the parietal lobes. Neuropsychologia 47:1449–1459.
Haggard P (2008) Human volition: towards a neuroscience of will. Nat Rev Neurosci 9:934–946.
Hayes SM, Ryan L, Schnyer DM, Nadel L (2004) An fMRI study of episodic memory: retrieval of object, spatial, and temporal information. Behav Neurosci 118:885–896.
Herbart JF (1825) Psychologie als Wissenschaft neu gegründet auf Erfahrung, Metaphysik und Mathematik [Psychology as a Science Newly Founded on Experience, Metaphysics, and Mathematics]. Königsberg: August Wilhelm Unzer.
Herwig A, Waszak F (2012) Action–effect bindings and ideomotor learning in intention- and stimulus-based actions. Front Psychol 3:444.
Herwig A, Prinz W, Waszak F (2007) Two modes of sensorimotor integration in intention-based and stimulus-based actions. Q J Exp Psychol 60:1540–1554.
Hoffmann J, Lenhard A, Sebald A, Pfister R (2009) Movements or targets: What makes an action in action–effect learning? Q J Exp Psychol 62:2433–2449.
Hommel B, Müsseler J, Aschersleben G, Prinz W (2001) The theory of event coding (TEC): a framework for perception and action planning. Behav Brain Sci 24:849–878.
Hubbard J, Gazzaley A, Morsella E (2011) Traditional response interference effects from anticipated action outcomes: a response–effect compatibility paradigm. Acta Psychol 138:106–110.
Jahanshahi M, Jenkins IH, Brown RG, Mardsen CD, Passingham RE, Brooks DJ (1995) Self-initiated versus externally triggered movements: I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. Brain 118:913–933.
Janczyk M, Skirde S, Weigelt M, Kunde W (2009) Visual and tactile action effects determine bimanual coordination performance. Human Mov Sci 28:437–449.
Karch S, Feuerecker R, Leicht G, Meindl T, Hantschk I, Kirsch V, Ertl M, Lutz J, Pogarell O, Mulert C (2010) Separating distinct aspects of the voluntary selection between response alternatives: N2- and P3-related BOLD responses. NeuroImage 51:356–364.
Karnath HO, Ferber S, Himmelbach M (2001) Spatial awareness is a function of the temporal not the posterior parietal lobe. Nature 411:950–953.
Kerns JG et al (2004) Anterior cingulate conflict monitoring and adjustments in control. Science 303:1023–1026.
Kühn S, Seurinck R, Fias W, Waszak F (2010) The internal anticipation of sensory action effects: When action induces FFA and PPA activity. Front Hum Neurosci 4:1–7.
Kühn S, Keizer A, Rombouts SA, Hommel B (2011) The functional and neural mechanism of action preparation: roles of EBA and FFA in voluntary action control. J Cogn Neurosci 23:214–220.
Kunde W (2001) Response–effect compatibility in manual choice reaction tasks. J Exp Psychol 27:387–394.
Kunde W, Koch I, Hoffmann J (2004) Anticipated action effects affect the selection, initiation, and execution of actions. Q J Exp Psychol A57:87–106.
Melcher T, Weidema M, Eenshuistra RM, Hommel B, Gruber O (2008) The neural substrate of the ideomotor principle: an event-related fMRI analysis. NeuroImage 39:1274–1288.
Melcher T, Winter D, Hommel B, Pfister R, Dechent P, Gruber O (2013) The neural substrate of the ideomotor principle revisited: evidence for asymmetries in action–effect learning. Neuroscience 231:13–27.
Pesaran B, Nelson MJ, Andersen RA (2008) Free choice activates a decision circuit between frontal and parietal cortex. Nature 453:406–409.
Pfister R, Kunde W (2013) Dissecting the response in response–effect compatibility. Exp Brain Res 224:647–655.
Pfister R, Kiesel A, Melcher T (2010) Adaptive control of ideomotor effect anticipations. Acta Psychol 135:316–322.
Pfister R, Kiesel A, Hoffmann J (2011) Learning at any rate: action–effect learning for stimulus-based actions. Psychol Res 75:61–65.
Pfister R, Schwarz KA, Janczyk M (2012) Ubi irritatio, ibi affluxus: a 19th century perspective on haemodynamic brain activity. Cortex 48:1061–1063.
Pfister R, Dignath D, Hommel B, Kunde W (2013a) It takes two to imitate: anticipation and imitation in social interaction. Psychol Sci 24:2117–2121.
Pfister R, Janczyk M, Gressmann M, Fournier LR, Kunde W (2013b) Good vibrations? Vibrotactile self-stimulation reveals anticipation of body-related action effects in motor control. Exp Brain Res. http://dx.doi.org/10.1007/s00221-013-3796-6.
Rieger M (2007) Letters as visual action–effects in skilled typing. Acta Psychol 126:138–153.
Rizzolatti G, Craighero L (2004) The mirror-neuron system. Ann Rev Neurosci 27:169–192.
Rizzolatti G, Matelli M (2003) Two different streams from the dorsal visual system: anatomy and functions. Exp Brain Res 153:146–157.
Rowe JB, Hughes L, Nimmo-Smith I (2010) Action selection: a race model for selected and non-selected actions distinguishes the contribution of premotor and prefrontal areas. NeuroImage 51:888–896.
Ruge H, Müller SC, Braver TS (2010) Anticipating the consequences of action: an fMRI study of intention-based task preparation. Psychophysiology 47:1019–1027.
Shin YK, Proctor RW, Capaldi EJ (2010) A review of contemporary ideomotor theory. Psychol Bull 136:943–974.
Sirigu A, Daprati E, Ciancia S, Giraux P, Nighoghossian N, Posada A, Haggard P (2004) Altered awareness of voluntary action after damage to the parietal cortex. Nat Neurosci 7:80–85.
Spengler S, von Cramon YD, Brass M (2009) Was it me or was it you? How the sense of agency originates from ideomotor learning revealed by fMRI. NeuroImage 46:290–298.
Wolfensteller U, Ruge H (2011) On the timescale of stimulus-based action–effect learning. Q J Exp Psychol 64:1273–1289.
Wolpert DM, Ghahramani Z (2000) Computational principles of movement neuroscience. Nat Neurosci 3:1212–1217.
Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269:1880–1882.
Wolpert DM, Goodbody SJ, Husain M (1998) Maintaining internal representations: the role of the human superior parietal lobe. Nat Neurosci 1:529–533.
Zwosta K, Ruge H, Wolfensteller U (2013) No anticipation without intention: response–effect compatibility in effect-based and stimulus-based actions. Acta Psychol 144:628–634.

(Accepted 27 November 2013)
(Available online 9 December 2013)