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.

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
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