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Pinpointing ideomotor effect anticipations in the human brain

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„Regarding the psychological possibility of the mind intentionally using the body as an instrument for acting […], it seems worthwhile to shed some more light on this fundamental matter concurrently from the psychological and the physiological perspective." (Herbart, 1825, pp. 462-463; translated by the author; see below for the original wording).

"Zwar schon oben […] ist über die psychologische Möglichkeit, dass die Seele im Handeln sich des Leibes absichtlich als eines Werkzeuges bediene, eine kurze Andeutung gegeben; allein es scheint passend, am gegenwärtigen Orte diesen wichtigen Gegenstand etwas ausführlicher, zugleich von der psychologischen und der physiologischen Seite, zu beleuchten."
(Herbart, 1825, pp. 462-463).

Johann Friedrich

Herbart (1776 – 1841)

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ZUSAMMENFASSUNG

Fast zwei Jahrhunderte nachdem Johann Friedrich Herbart die ersten Vorstellungen dessen formulierte, was später als ideomotorisches Prinzip bekannt werden sollte, haben wir noch immer kein umfassendes Verständnis derjenigen Mechanismen erarbeitet, die Ideen einerseits und motorische Impulse andererseits miteinander verbinden. Die vorliegende Arbeit schließt zwei empirische Lücken dieser Ideomotorikforschung.

Experiment 1 und 2 untersuchten, ob das ideomotorische Prinzip auch dann einen validen Ansatz der Handlungssteuerung darstellt, wenn Handlungs-Effekt-Beziehungen einem schnellen Wechsel unterworfen sind – Bedingungen, die deutlich alltagsnäher sind als die Paradigmen früherer Studien. Hierfür wurde ein Aktions-Effekt-(A-E)-Kompatibilitätsparadigma mit kontextspezifischen A-E-Beziehungen eingesetzt. Die Probanden betätigten eine linke oder rechte Taste und erzeugten hierdurch räumlich kompatible, neutrale oder inkompatible Handlungseffekte. Experiment 1 verglich zwei Experimentalgruppen, die ihre Handlungen entweder selbst wählten oder auf ein imperatives Signal reagierten. Übereinstimmend mit der Theorie der Handlungskontrollmodi (action control modes) traten A-E-Kompatibilitätseffekte nur für frei gewählte, nicht aber für reaktive Handlungen auf. Experiment 2 zeigte weiterhin, dass A-E-Kompatibilitätseffekte auch für beide Arten von Handlungen resultieren können, wenn frei gewählte und reaktive Handlungen gleich häufig in einem Experimentalblock auftreten. Diese Befunde legen

nahe, dass das ideomotorische Prinzip auch Bewegungskontrolle unter solchen realitätsnäheren Bedingungen erklären kann.

Experiment 3 und 4 passten das verwendete Paradigma für eine Untersuchung mittels funktioneller Magnetresonanztomographie (fMRT) an. Durch einen relativ kleinen Anteil von frei gewählten Handlungen erzielten wir A-E-Kompatibilitätseffekte für frei gewählte aber nicht für reaktive Handlungen, obwohl beide Arten von Handlungen im selben Experimentalblock auftraten. Als Indikatoren ideomotorischer Handlungskontrolle wurden die individuellen Kompatibilitätseffekte als Regressoren in der fMRT-Auswertung eingesetzt. Im Kontrast frei gewählter und reaktiver Handlungen korrelierte der Verhaltenseffekt unter anderem mit Aktivität der Hippocampusformation und dem inferioren Parietallappen. Diese Analyse stellt den ersten neurophysiologischen Nachweis von Handlungskontrolle über die Antizipation von Handlungseffekten dar, wie sie durch das ideomotorische Prinzip postuliert wird.

SUMMARY

Nearly two centuries after Johann Friedrich Herbart formulated the first concepts of what should later be called the ideomotor principle of action, we still do not have a precise understanding of the mechanisms linking ideas on the one hand and motor commands on the other hand. The present series of experiments closes two empirical gaps in ideomotor research.

Experiment 1 and 2 investigated whether ideomotor theory accounts for action control under rapidly varying action-effect relations, a setting that comes closer to daily actions than previous studies did. To this end, I employed a response-effect (R-E) compatibility design with context-specific R-E relations that varied trial-to-trial. Participants pressed a left or right key and produced spatially compatible, neutral, or incompatible action effects. Experiment 1 compared two groups of participants that could either freely choose their actions or reacted to imperative stimuli. In accordance with the theory of action control modes, R-E compatibility effects only resulted for freely chosen actions whereas no effects occurred for forced choice reactions. Experiment 2 showed that R-E compatibility effects, however, can result for both types of action when free and forced choices occur equally often in the same experimental block. Taken together, these findings suggest that ideomotor theory can indeed account for action control under ecologically valid settings.

Experiment 3 and 4 modified the design in order to suit the demands of functional magnetic resonance imaging (fMRI). By using a relatively small proportion of free choice trials, R-E compatibility effects resulted only for free choice trials even though free and forced choice trials occurred in the same experimental block. This behavioural marker of effect anticipation then served as regressor for the fMRI response. Within the contrast of free versus forced choice trials, the behavioural effect correlated with the activity in several circumscribed regions, most importantly the hippocampal formation and the inferior parietal lobule. This analysis is the first neurophysiological demonstration of action control via action effect anticipations as suggested by ideo-motor theory.

IDEOMOTOR EFFECT ANTICIPATIONS – BEHAVIOURAL EVIDENCE

"We accept that we can will action, but cannot accomplish it ourselves, that rather a natural course completely independent from our will has linked our will and other conditions of our soul with mechanical necessity to changes of our body, from which movements of the limbs in certain amplitudes and directions must result independently. All that is left to us is to create the psychic states that these physical processes originate from, and from which they unfold, in agreement with our aims, following rules and mediated by processes all of which elude our consciousness."

Rudolf Herrmann Lotze (1817 – 1881)

(Lotze, 1852, p. 288; cited after Stock & Stock, 2004, p. 181)

1 Ideomotor Theory and Intentional Behaviour

The *ideomotor principle* addresses an inherent aspect of the fundamental mind-body problem: How can the mind exert control over the body? How can overt action originate from a subjective state of mind? How can our brain generate goal-directed, intentional behaviour?

In our daily life, we perform millions and billions of actions without being aware of the precise and reliable mechanisms that translate our countless goals into muscular activity. However, at a closer look, these ubiquitous mechanisms are far from trivial and challenge various scientific disciplines such as philosophy (e.g. Descartes, 1641; Popper & Eccles, 1977), psychology (Hoffmann, 1993; Prinz, 1987), robotics (Wolpert & Kawato, 1998), and neuroscience (Haggard, 2008; Wolpert & Ghahramani, 2000).

The ideomotor principle proposes an elegant and parsimonious solution to the question of how the mind can evoke overt action (Herbart, 1825; James, 1890; Lotze, 1852; for more recent formulations, see Greenwald, 1970a, 1970b; Hoffmann, 1993, 2003; Hoffmann et al., 2007; Hommel, 1998, 2003; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1987, 1990, 1997). According to the IMP, representations of motor patterns and contingently following effects are associated bidirectionally. Due to these bidirectional relations, anticipations of action effects gain the power to address the corresponding motor patterns and thus enable the agent to produce the appropriate action. The huge body of research examining bidirectional action-effect relations can be divided into two main types of studies concentrating on different aspects of ideomotor action: ideomotor-learning studies and effect-anticipation studies. In the following, I first provide an overview on effect-anticipation studies and then discuss several aspects of ideomotor learning afterwards.

1.1 Effect Anticipations in Action Control

Effect-anticipation studies focus on demonstrating that a mental representation of the effects is created prior to action execution. These effect anticipations influence various aspects of action control what can be directly assessed with response-effect (R-E) compatibility paradigms (Janczyk, Skirde, Weigelt, & Kunde, 2009; Keller & Koch, 2006, 2008; Koch & Kunde, 2002; Kunde, 2001, 2003; Kunde, Koch, & Hoffmann, 2004; Stöcker, Sebald, & Hoffmann, 2003; Rieger, 2007).

Investigations with the R-E-compatibility paradigm apply the same logic as stimulus-response (S-R) compatibility studies. That is, if stimuli and responses overlap on any dimension, responding is typically faster (and more accurate) if stimuli and responses share a feature on this dimension as compared to incompatible features on this dimension (e.g. Fitts & Seeger, 1953; Simon & Rudell, 1967; see Kornblum, Hasbroucq, & Osman, 1990 for an overview). For example, a right key press is performed faster in response to a stimulus that is presented in the right compared to the left visual field.

Now, if participants actually anticipate the effect of an action prior to action execution, similar compatibility phenomena are to be expected between anticipated effects and responses. For instance, Kunde (2001, Exp. 1) asked participants to press horizontally arranged keys in response to arbitrary target stimuli whereby each key press triggered a visual action effect. Crucially, the spatial compatibility of key location and effect location was varied in two conditions. In one condition, key location and effect location were compatible. That is, if a right key was pressed, the action effect appeared in the right visual field. In a second condition, key location and effect location were incompatible. That is, if a right key was pressed, the action effect appeared in the left visual field. Participants responded faster in the compatible condition than in the

incompatible condition. As both conditions employed identical target stimuli, this effect can only be attributed to the participants' anticipation of action effects, even though participants were not instructed to produce these effects (Kunde, 2001).

Similar R-E-compatibility effects were shown in a variety of settings not only with spatial compatibility but also with respect to other feature dimensions like intensity (Kunde, 2001, Exp. 2; Kunde et al., 2004), semantic category (Koch & Kunde, 2002), or temporal duration of actions and effects (Kunde, 2003). However, all these experiments varied R-E-compatibility in blocks, i.e. participants first experienced a homogeneous series of compatible R-E-mappings followed by a homogeneous series of incompatible mappings (or vice versa). This experimental procedure was explained in terms of methodological constraints: "R-E compatibility will only emerge with corresponding and noncorresponding R-E mappings blocked because only in this case the effects follow the responses consistently and can thus serve as a reliable mental cue to address a certain motor pattern." (Kunde, 2001, p. 393).

In contrast, more realistic day-to-day settings include rapidly varying relations between actions and effects. For example, while writing a text in a word processor, key presses of left-hand keys on the computer keyboard produce spatially compatible action effects at the beginning of a line (e.g. starting a new line with the letter "A" which appears on the left side of the monitor). However, action effects are spatially incompatible in the middle and especially at the end of the line (e.g. letter "A" on the right side of the monitor). Hence, assuming that preparation and execution of a specific action indeed depend on the anticipation of its effects, R-E compatibility effects may also emerge for rapidly varying R-E relations as long as effects are predictable due to the context.

Thus, the main goal of the present study is to investigate whether ideomotor effect anticipations also occur if action-effect relations vary trial-by-trial and the effects do not represent the primary action goal.[1] For this purpose, I employed a modified version of Kunde's (2001) experimental setting where the R-E-mapping changed on a trial-to-trial basis with a cue indicating the current R-E-mapping.

1.2 Intention in Ideomotor Learning

In addition, I present a second variation to Kunde's (2001) original paradigm by comparing freely chosen actions to forced choice actions which was derived from recent studies on ideomotor learning. In contrast to effect-anticipation studies, these studies focus on the impact of newly learned action-effect representations and typically apply two distinct experimental phases (Greenwald, 1970a). First, a learning phase is used to establish a relation between actions and following sensory effects where participants typically perform distinct actions, e.g. pressing a left or right key, and contingently produce distinct exteroceptive effects, e.g. a high or low pitch tone. In a subsequent test phase, the former action effects serve as target stimuli in a forced choice RT task. Participants are either instructed to respond with the action that formerly produced the stimulus or with the alternative action that formerly produced the alternative stimulus. Commonly, responses are faster when the effect-response mapping of the test phase is the same as the response-effect mapping of the preceding learning phase as compared to a reversed mapping (e.g. Elsner & Hommel, 2001).

[1] Please note that two previous studies by Ansorge (2002) and Kiesel and Hoffmann (2004) observed R-E compatibility effects only when participants were explicitly instructed to produce the context-specific effect. I refer back to these studies in the discussion in chapter 4.

This non-reversal advantage was demonstrated for various action effects (Beckers, De Houwer, & Eelen, 2002; Drost, Rieger, Brass, Gunter, & Prinz, 2005a, b; Hoffmann, Lenhard, Sebald, & Pfister, 2009; Hommel, Alonso, & Fuentes, 2003; Rieger, 2004, 2007) and for different age groups (Eenshuistra, Weidema, & Hommel, 2004; Elsner & Hommel, 2001, 2004; Kray, Eenshuistra, Kerstner, Weidema, & Hommel, 2006). Additionally, neuroimaging studies identified the supplementary motor area (SMA) and the hippocampus as central neuroanatomical structures for action control via learned ideomotor associations (Elsner et al. 2002; Melcher, Weidema, Eenshuistra, Hommel, & Gruber, 2008).

However, Herwig, Prinz, and Waszak (2007) demonstrated that the well-established non-reversal advantage depends on the task instructed in the learning phase. In a series of experiments, they replicated the conditions of Elsner and Hommel (2001) but altered the learning phase for several groups of participants. While the participants of Elsner and Hommel experienced a free choice between two response alternatives during the learning phase, the altered learning phase of Herwig and colleagues consisted of forced choice trials only, i.e. participants saw an imperative stimulus that instructed a specific response. In this latter case, the non-reversal advantage as indication of ideomotor learning was absent.

To explain this difference, these authors assume that action-effect learning as well as action control rely on fundamentally different systems (action control modes) when reactions are carried out in response to exogenous stimuli (*stimulus-based*) as opposed to endogenously driven actions (*intention-based*). Only intention-based actions are conceptualized to rely on ideomotor-mechanisms including the prominent role of action-effect associations. In the intention-based mode, motor commands are thus selected by anticipating to-be-expected action effects. In contrast, stimulus-based

actions are conceptualized to rely on stimulus-response associations. In the stimulus-based mode, motor commands are thus selected according to learned responses to a stimulus (see Knuf, Aschersleben, & Prinz, 2001 and Pfister, Kiesel, & Hoffmann, in press, for a related discussion). The hypothesized difference between stimulus-based and intention-based actions was demonstrated in various studies. For instance, stimulus-based actions are typically executed faster and elicit different EEG-patterns than intention-based actions (Keller et al., 2006; Waszak et al., 2005), and they consistently fail to produce non-reversal advantages in ideomotor-learning studies (Herwig et al., 2007, Herwig & Waszak, 2009).

As a second goal, the present experiments were designed to investigate whether the anticipation of action effects is moderated by these modes of action control. Given the manifest differences between stimulus-based and intention-based action control, I expected R-E-compatibility effects to result when participants act in an intention-based action control mode whereas I did not expect R-E compatibility effects for the stimulus-based action control mode. Two experiments tested these predictions.

2 Experiment 1: Effect Anticipations under Rapdily Varying R-E-Relations

To investigate R-E compatibility effects for rapidly varying R-E relations, I applied a simplified version of Kunde's (2001) setting. Participants either pressed a left or right response key that triggered a visual effect on the monitor. Left and right key presses either induced left and right visual effects (compatible R-E relation) or right and left visual effects, respectively (incompatible R-E relation). The R-E-compatibility varied trial-by trial whereby a cue informed about the current relation. In addition to spatially compatible and spatially incompatible action effects, I also included spatially neutral, i.e. neither compatible nor incompatible action effects that were not perfectly predictable (see **Figure 1**).

In Experiment 1, the action control mode was varied between-subjects (cf. Herwig et al., 2007). The stimulus-based mode was implemented by forced choice reactions to imperative stimuli (*forced choice group* hereafter) whereas the intention-based mode was implemented by asking the participants to freely choose between the two response alternatives throughout the experiment (*free choice group* hereafter). Furthermore, I added nogo-trials in the free choice condition to discourage participants to preliminarily prepare an action (see e.g., Kunde, 2001, Exp. 3). I expected an R-E-compatibility effect for the free choice group with faster reactions under compatible than incompatible R-E mappings (Kunde, 2001), while I did not expect an R-E compatibility effect for the forced choice group.

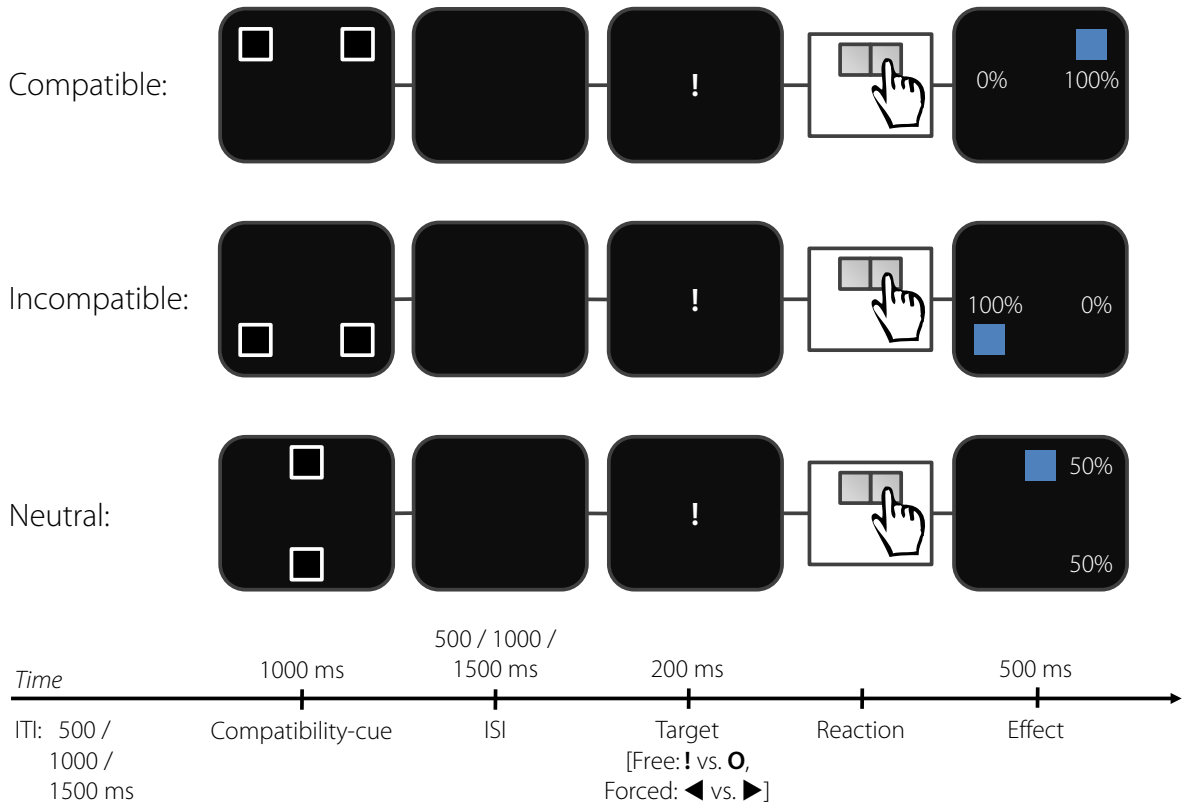

Figure 1. Basic experimental setup of both experiments, including a trial-by-trial variation of response-effect (R-E) compatibility (compatible vs. neutral vs. incompatible) as well as the implementation of free and forced choice trials. Each trial started with a cue (white boxes) that informed about the current R-E compatibility relation (100% valid). Independent of the cue, participants were instructed to press a key in response to a target stimulus. The target either instructed free choice (exclamation mark) or forced choice responses (left or right arrows) and participants had to respond within 1000 ms after target onset. In Experiment 1, free and forced choices were varied between-subjects (including nogo-trials for the free choice group as indicated by circles as targets) whereas they were varied within-subjects in Experiment 2 (without nogo-trials). Correct responses triggered the presentation of a blue (90%) or orange (10%) square. In case of orange squares (deviant effects), participants had to respond again by pressing both keys simultaneously. The figure depicts a free choice trial where the participant chooses to press a right key in a trial with compatible, incompatible, or neutral R-E-mapping. The assignment of upper vs. lower cues to compatible vs. incompatible R-E-mappings was counterbalanced across participants.

2.1 Method

2.1.1 Participants

Twenty-four undergraduate students at the University of Würzburg (9 males; 3 left-handed) were recruited and received either course credit or were paid for participation. The mean age was 23.83 years (*SD* = 3.42), participants reported normal or corrected-to normal vision and were naive as to the purpose of the experiment.

2.1.2 Apparatus and Stimuli

Stimuli were displayed on a 17'' monitor at a refresh rate of 75 Hz and responses were collected by two external keys that were connected to an IBM-compatible PC. The keys were arranged horizontally with an intercenter distance of 15 cm and key locations were matched to the locations of cue boxes and effect squares in compatible and incompatible trials (see **Figure 1**). Cue boxes, presented in white, and effect squares, presented in blue or orange, measured 2.5 cm x 2.5 cm. The two cue boxes indicating neutral trials were shown in the centre 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) and compatibility conditions (compatible vs. incompatible) was counterbalanced across participants so that cue boxes in the upper half indicated compatible trials for one half of the participants and incompatible trials for the other half. Target stimuli (i.e. left and right arrows, exclamation marks, and circles) were displayed in a 24 point font in the centre of the screen (arrows: 0.5 cm x 0.6 cm, exclamation mark: 0.1 cm x 0.6 cm, circle: 0.6 x 0.6 cm).

2.1.3 Procedure

Each trial started with the presentation of a cue that informed about possible effect locations and R-E-compatibility relations (100% valid; **Figure 1**). The compatibility cue was presented for 1000 ms followed by a blank screen with a variable duration of either 500, 1000, or 1500 ms. Then, the target stimulus was displayed for 200 ms and participants had to respond within 1000 ms after target onset. For the forced choice group, the target stimulus was a left or right arrow instructing either a left or a right key press whereas for the free choice group, an exclamation mark instructed participants to freely choose one of the two keys while a circle indicated a nogo-trial. 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 randomly presented either in the top or bottom centre.

To increase the salience of the effect squares, the colour of the effect square was orange in 10% of the trials (referred to as deviant effects hereafter). In this case, participants were to press both keys simultaneously (maximum offset: 50 ms) and as fast as possible with a maximum RT of 1500 ms after effect onset. The next trial started after a variable ITI of 500, 1000, or 1500 ms. Responses prior to the target stimulus, wrong key presses in forced choice trials, non-simultaneous key presses on deviant effects, and key presses in response to normal effects stopped the trial immediately and an error message indicating the type of error appeared for 1000 ms.

Participants worked through four training blocks and six test blocks. The first three training blocks contained only one compatibility condition each whereby the order of conditions was counterbalanced across participants. The fourth training block as well as each test block contained all compatibility conditions. For the forced choice group, blocks consisted of 46 trials each. For this group, the first three training blocks consisted of 50% free and 50% forced choice trials whereas the last training block as well as the test blocks only contained forced choice trials (14 trials of each compatibility condition with normal effects and four randomly distributed deviant effects). For the free choice group, blocks consisted of 66 trials. For this group, the first three training blocks also consisted of 50% free and 50% forced choice trials to provide similar learning experiences for both groups. Forced choice trials were replaced by nogo-trials in the fourth training block and the six test blocks so that these blocks consisted of 50% nogo-trials and 50% free choice trials (10 trials of each compatibility condition with normal effects, and 3 randomly distributed deviant effects).

2.2 Results

Trials with responses prior to the target or RT < 100 ms (0.4%), response omissions (0.3%), wrong key presses in forced choice trials (1.4%), deviant missings (0.3%), non-simultaneous key presses to deviant effects (0.6%), and key presses in reaction to normal effects (0.5%) were excluded from data analysis (3.5% in total). I aggregated the remaining RTs of the six test blocks for each combination of the factors compatibility (compatible vs. neutral vs. incompatible) and choice (free vs. forced). Trials with deviant effects were included in the analysis as responses occurred prior to effect onset. Additional analysis, however, revealed a similar pattern of results when deviant trials, trials following deviant effects, or both were excluded from the analysis. All within-subjects ANOVAs were computed as multivariate tests.

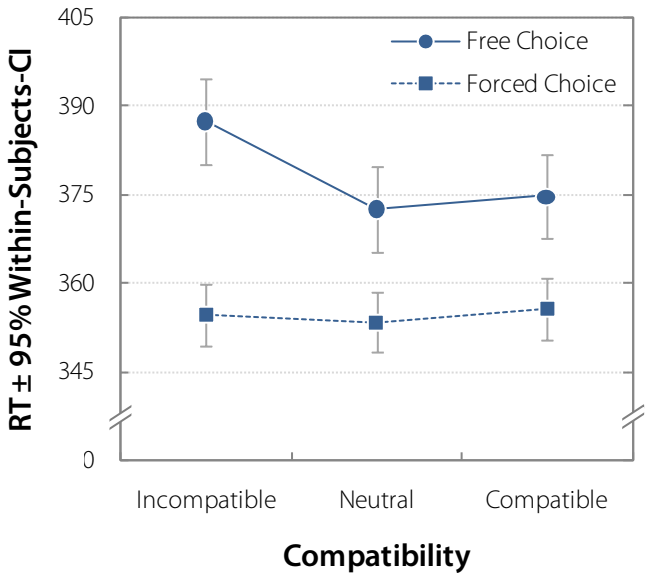

Figure 2. Mean RTs in Experiment 1 as a function of the within-subjects factor R-E compatibility and the between-subjects factor choice. Error bars represent within-subjects confidence intervals (Loftus & Masson, 1994) that were computed seperately for both choice groups.

2.2.1 Compatibility effects in both groups

A 2 (group) x 3 (compatibility) split-plot ANOVA was conducted on the mean RTs of the participants (see **Figure 2**). The within-subjects factor compatibility influenced RTs significantly, $F(2, 21) = 4.18$, $p = .030$, $\eta_p^2 = 0.28$, and its influence was confined to the free choice group as qualified by a significant interaction between compatibility and group, $F(2, 21) = 4.23$, $p = .029$, $\eta_p^2 = 0.29$. Even though a notable RT difference of 24 ms was found between both groups, the factor group was not statistically significant, $F(1, 22) = 1.58$, $p = .222$, $\eta_p^2 = 0.07$.

Separate within-subjects ANOVAs for both groups showed no effect of compatibility for the forced choice group, $F(2, 10) = 0.18$, $p = .840$, $\eta_p^2 = 0.03$ whereas a significant effect of compatibility was present for the free choice group, $F(2, 10) = 7.59$, $p = .010$, $\eta_p^2 = 0.60$. Here, the direct comparison of compatible and incompatible trials with a two-tailed t-test reflected the results of the omnibus test with RTs being faster for compatible trials, $t(11) = 3.49$, $p = .005$, d = 1.49.

2.2.2 Neutral effects

The impact of neutral effects was assessed by pairwise comparisons with both, compatible and incompatible trials by means of separate two-tailed t-tests for the free choice group. Here, a significant difference resulted when comparing neutral to incompatible trials, $t(11) = 2.85$, $p = .016$, d = 1.21, whereas neutral an compatible trials did not differ significantly, $t(11) = -0.38$, $p = .713$, d = -0.16.

2.2.3 Exploratory sequence analysis

The present design allows further analyses targeting the sequential modulation of the compatibility effect. Therefore, the data of the free choice group were subjected to a new 3 (compatibility) x 3 (compatibility in trial n-1) within-subjects ANOVA while trials after nogo-trials were excluded from this analysis. Here, the factor compatibility was significant, $F(2, 10) = 5.38$, $p = .026$, $\eta_p^2 = 0.52$ while neither the compatibility in the preceding trial nor the interaction approached significance (both p's > .306). However, because this procedure resulted in a small number of data points for some participants (n ≥ 11 trials per condition), this analysis is explicitly marked as exploratory.

2.3 Discussion

In this first experiment, I investigated effects ideomotor effect anticipations under rapidly varying R-E compatibility conditions in (a) an intention-based mode when participants carried out free choice responses and (b) a stimulus-based mode when participants carried out forced choice responses to imperative stimuli. As expected, I found a significant interaction between R-E compatibility and control mode with only participants of the free choice group exhibiting a reliable R-E-compatibility effect. In line with recent findings and related theoretical assumptions (Herwig et al., 2007; Keller et al., 2006; Waszak et al., 2005), this pattern of results clearly indicates that ideomotor effect anticipations are an integral part of internally guided actions whereas externally prescribed actions do arguably not – or at least to a substantially lesser degree – rely on this control mechanism.

Currently the concept of action control modes is not well understood. For example it is unclear whether action control modes switch rapidly between stimulus-based and intention-based if free and forced choice trials occur in mixed blocks. Alternatively action control modes may be conceptualized as enduring cognitive states that are maintained over a longer period of time (cf. Pfister et al, in press). Ideomotor learning studies consistently report evidence for ideomotor action-effect associations in pure forced choice test phases that were preceded by pure free choice learning phases (e.g. Elsner & Hommel, 2001; Hoffmann et al., 2009; Hommel et al., 2003; Melcher, Weidema, Eenshuistra, Hommel, & Gruber, 2008). This pattern of results might indicate that an enduring intention-based action control mode was established in the free choice learning phase and was carried over to the forced choice test phase so that action-effect associations could influence the participants' behaviour. Furthermore, this finding might indicate that the intention-based action control mode is the dominant mode as it is also

applied to forced choice actions instead of switching between both modes. Thus, if action control modes can indeed be conceptualised as enduring cognitive states with the intention-based mode being dominant over the stimulus-based mode, the same line of argument should hold true for effect anticipations in R-E-compatibility designs. Experiment 2 addressed this speculation.

3 Experiment 2: Enduring Action Control Modes

Experiment 2, tested the speculation of action control modes being enduring cognitive states. To this end, I adopted the design of Experiment 1 (**Figure 1**) but varied free and forced choices trial-by-trial rather than as a between-subjects factor. In this design, I expected an R-E-compatibility effect to result for both, free and forced choice actions.

3.1 Method

3.1.1 Participants

Twelve undergraduate students at the University of Würzburg (3 males, all right-handed) were recruited and received either course credit or were paid for participation. The mean age was 24.58 years (*SD* = 4.61), participants reported normal or corrected-to normal vision and were naive as to the purpose of the experiment.

3.1.2 Apparatus, Stimuli, and Procedure

Experiment 2 used the same paradigm as Experiment 1 (see **Figure 1**) with the following modifications. Participants experienced free and forced choice trials equally often and throughout the experiment. Again, the experiment consisted of four training blocks and six test blocks, each of them comprising 66 trials (10 free and 10 forced choice trials with normal effects for each compatibility condition and 6 randomly distributed deviant effects). No nogo-trials were used.

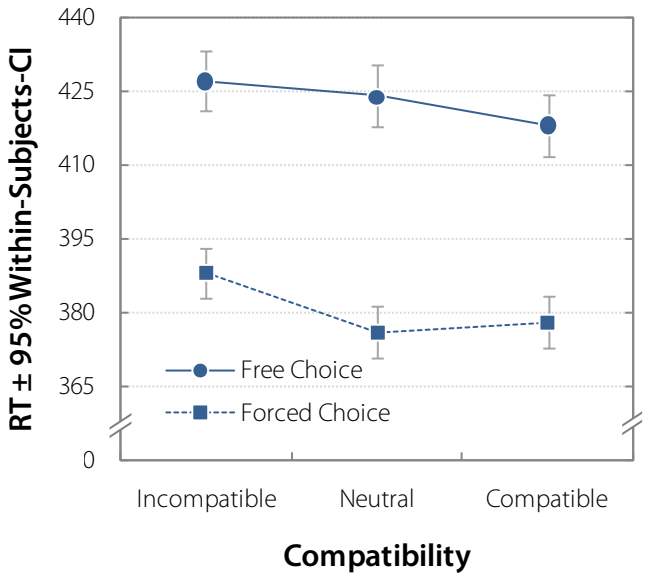

Figure 3. Mean RTs in Experiment 2 as a function of both within-subjects factors, R-E compatibility and choice. Error bars represent within-subjects confidence intervals (Loftus & Masson, 1994); to allow a better comparison with Experiment 1, confidence intervals were computed seperately for both choice conditions.

3.2 Results

As for Experiment 1, trials with responses prior to the target or RT < 100 ms (0.6%), response omissions (0.9%), wrong key presses in forced choice trials (2.4%), deviant missings (0.1%), non-simultaneous key presses to deviant effects (0.9%), and key presses in reaction to normal effects (1.2%) were excluded from data analysis (6.1% in total).

3.2.1 Compatibility effects

A 2 (choice) x 3 (compatibility) within-subjects ANOVA was conducted on the mean RTs of the participants (**Figure 3**) and both, the main effect of compatibility, $F(2, 10) = 5.04$, $p = .031$, $\eta_p^2 = 0.27$, and the main effect of choice, $F(1, 11) = 12.99$, $p =$

.004, η_p^2 = 0.54, were significant. However, the interaction of both factors did not approach significance (F < 1). As for the free choice group of Experiment 1, a direct comparison of compatible and incompatible trials resulted in significantly faster RTs for compatible trials, $t(11) = 2.63$, $p = .023$, d = 1.08.

3.2.2 Neutral effects

The impact of neutral effects was again assessed by pairwise comparisons with both, compatible and incompatible effects by means of separate two-tailed t-tests. In contrast to Experiment 1, neutral trials were situated between both other compatibility conditions so that neither the difference between incompatible and neutral trials, $t(11) = 1.61$, $p = .136$, d = 0.66, nor the difference between neutral and compatible trials was significant, $t(11) = 0.92$, $p = .374$, d = 0.38.

3.3 Discussion

Experiment 2 extended the findings of Experiment 1 to situations with free and forced choices occurring intermixed in one experimental block. Here, equally strong R-E compatibility effects resulted for both, free and forced choice trials. Thus, it seems that participants anticipated the effects according to the current context in order to initiate the respective response in free as well as forced choice trials. I take this as evidence that the participants adopted an enduring intention-based action control mode when free and forced choice trials occur randomly intermixed.

An alternative to the present interpretation is a possible co-occurrence of R-E compatibility and stimulus-stimulus (S-S) compatibility. S-S compatibility could have been evoked by the arrows that were used as target stimuli in forced choice trials because symbolic cues are also able to activate the spatial dimension (Reeve & Proctor, 1990; Wascher, Reinhard, Wauschkuhn, & Verleger, 1999). However, this alternative

interpretation is not consistent with two findings of the present experiment. First, R-E-compatibility effects were also obtained in free choice trials where S-S compatibility effects were definitely absent and, second, no R-E compatibility effects were obtained for the forced choice group of Experiment 1 where S-S compatibility could exert its influence in every trial. Thus, the observed compatibility effect for forced choice trials arguably reflects the anticipation of compatible and incompatible response effects.

4 Discussion: Action Control Modes and Ideomotor Effect Anticipations

The present experiments investigated rapidly varying, context-dependent effect anticipations in order to extend the empirical evidence for ideomotor action control to these more natural settings. In each trial, a cue informed participants about the current compatibility relation between responses and effects while the response was triggered by a free or forced choice target stimulus. To assess the impact of R-E-compatibility, reaction times in compatible trials were compared to reaction times in incompatible trials (cf. Kunde, 2001). Additionally, I assessed the role of different modes of action control (stimulus-based versus intention-based mode; Herwig et al., 2007; Herwig & Waszak, 2009). Action control in the stimulus-based mode is conceptualized to be based on S-R associations whereas action control in the intention-based mode is conceptualized to be based on ideomotor mechanisms including the prominent contribution of effect anticipations. In Experiment 1, I investigated ideomotor effect anticipations separately in stimulus-based and intention-based action control, which was implemented in otherwise comparable groups working under forced-choice and free-choice conditions, respectively (cf. Herwig et al., 2007).

A substantial R-E compatibility effect was observed for the free choice group whereas the forced choice group did not show a difference between compatible and incompatible response-effect mappings. These results indicate that R-E compatibility effects can indeed be induced on a trial-to-trial basis if an intention-based action control mode is adopted under free choice conditions. In Experiment 2, I elaborated whether participants adopt an enduring intention-based action control mode when free and forced choice trials switch randomly. In this setting I observed R-E-compatibility effects

for free choice responses and for forced choice responses. Thus, R-E compatibility effects can also result for forced choice actions if participants are in an action control mode that fosters anticipation of exteroceptive action effects. I will refer back to this issue later.

Taken together, the present findings indicate that the ideomotor principle provides a valid account for action control under ecologically valid conditions, i.e. effect anticipations are used for action initiation and execution not only under constant but also under rapidly varying response-effect relations. Furthermore, ideomotor action control can be applied to endogenously (free choice) as well as exogenously prescribed (forced choice) actions, given that an intention-based action control mode is adopted.

The assumed role of intention and intention-based action control is in line with findings on S-R compatibility effects, where specific instructions were used to induce an intention-based action control mode (Ansorge & Wühr, 2004; Guiard, 1983; Hommel, 1993). For instance, an intention-based action control mode was shown to reverse the typical Simon effect (Simon, 1967) if intended target locations and respective motor commands counteracted (Hommel, 1993).

Further evidence for a fundamental difference between intention-based and stimulus-based actions is provided by neuroanatomical and neurophysiological studies. Most importantly, both action control modes seem to be based on distinct neuro-anatomical systems (see Haggard, 2008 for an overview). Intention-based actions were related primarily to fronto-striatal areas such as the dorso-lateral prefrontal cortex and especially the supplementary motor area (SMA; Cunnington, Windischberger, Deeke, & Moser, 2002; Jahanshahi et al., 1995; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000; Müller, Brass, Waszak, & Prinz, 2007, Wiese et al., 2004), the basal ganglia (Francois-Brosseau et al., 2009), and possibly parietal association cortices

(Desmurget et al., 2009). In contrast, stimulus-based actions seem to depend on specialized task-dependent systems (Toni, Rushworth, & Passingham, 2001). Neuro-anatomical and neurophysiological differences between both action control modes are also mirrored in differential patterns of muscular activity (EMG signal) for intention-based and stimulus-based actions (Obhi & Haggard, 2004).

Furthermore, the motor system for intention-based actions seems to be shielded against possible influences of stimulus-response associations. For instance, preparing an intention-based action reduced general "reactivity" (Astor-Jack & Haggard, 2005). Astor-Jack and Haggard (2005) asked their participants to press a key at a freely chosen time in a given trial. In some trials, however, action preparation was interrupted by a target stimulus forcing the participants to perform the partly-prepared key press as fast as possible. Interestingly, participants responded slower to the target stimulus when they had already prepared the same response in the free choice condition compared to a condition in which participants always responded to the target stimulus without any self-intended action preparation. Astor-Jack and Haggard conclude that the observed response costs mirror a process of deactivating the intention-based system and activating the stimulus-based system.

At the moment, however, it seems unclear, when exactly participants adopt intention-based or stimulus-based action control modes. According to Herwig and colleagues (2007), free choice trials induce an intention-based action control mode while forced choice trials induce a stimulus-based action control mode. Yet, also forced choice conditions reveal R-E compatibility and thus, participants are assumed to anticipate to-be expected effects also in forced choice conditions. Currently, it seems that R-E compatibility effects can also occur when the R-E relation remains constant over blocks of forced choice trials (e.g. Kunde 2001, 2003; Koch & Kunde, 2002). Thus, the

easier participants can acquire R-E relations the more likely they rely on effect anticipations to initiate a response.

Furthermore, to the best of my knowledge, there are two studies demonstrating R-E compatibility effects for forced choice responses when the R-E relations varied context-specifically (Ansorge, 2002; Kiesel & Hoffmann, 2004). Kiesel and Hoffmann (2004) observed an influence of context-specific and arbitrary effects in a task switching setting. In these experiments, participants were to press a bottom left or top right key (diagonal arrangement; cf. Meiran, 1996) in response to a forced-choice target stimulus that appeared in one of the quadrants of a large fixation cross. Participants either responded according to the horizontal (task A) or vertical (task B) position of the target stimulus. Square brackets presented to the left and right or the top and bottom of the screen indicated whether the horizontal or vertical task was required. After a correct response, the round target stimulus moved slowly versus fast towards the nearest square bracket while the speed entirely depended on the task. Responses were faster, when a fast movement was to follow as compared to a slow movement even though the movement speed was irrelevant to the task at hand. Yet, in this setting, the effects were very salient because Kiesel and Hoffmann (2004) referred to their target stimulus as a ball and instructed their participants to "shoot the ball into the nearest goal" (p. 157). Thus, it seems that instructing participants to intend an effect boosters effect anticipations even in settings with context-specific R-E assignments/relations. This conclusion fits nicely to the second study demonstrating R-E compatibility effects when varying R-E assignments trial-by trial. Ansorge (2002) applied a somewhat similar design as the present study. In each trial, a cue informed participants about compatible or incompatible response-effect relations and a forced choice response had to be performed after an arbitrary target stimulus appeared on the center of the screen. After

a left or right key press, the target stimulus was relocated to the left or right side of the monitor, leading to compatible or incompatible effects. Ansorge (2002) found R-E compatibility effects only if participants were explicitly instructed to produce left or right effects (for similar findings see Kunde, Krauss, & Weigelt, 2009; Kunde & Weigelt, 2005) but not if participants were told to respond according to the target stimulus and experienced the very same effects afterwards. This latter condition corresponds to forced choice group of the present study and I thus conjecture that participants in Ansorge's study may also have adopted a stimulus-based action control mode.

To sum up, the present experiments demonstrated trial-based response-effect compatibility effects and thus extend the empirical evidence for the ideomotor principle to a setting with higher ecological validity. Trial-based response-effect compatibility effects were obtained as long as participants established an intention-based action control mode because of the possibility to freely choose among several actions. If participants responded in a stimulus-based action control mode because they responded exclusively in forced choice conditions, trial-based response-effect compatibility effects were eliminated.

PINPOINTING EFFECT ANTICIPATIONS IN THE HUMAN BRAIN

Thomas Laycock
(1812-1876)

„Those substrata, the teleorganic changes of which hypothetically correspond to notional states of consciousness, I termed *ideagenic* substrata; those, the teleorganic changes of which correspond hypothetically to motor phenomena, I termed *kinetic* substrata; and I pointed out certain general laws as to their origin, development, latency, and transmission to offspring, in explanation of a great variety of psychal phenomena of the instinctive character." (Laycock, 1860, p. 11).

Speculations about possible neural mechanisms underlying ideomotor action control can be traced back to the very origins of ideomotor theory (see Stock & Stock, 2004 for an overview). In analogy to Herbart's (1825) classical speculation, Thomas Laycock (1845, 1860) postulated two discrete substances in the mammalian nervous system: ideagenic and kinetic substrates with the former hosting thoughts and volition and the latter producing overt action. He assumed that ideagenic substrates are connected to kinetic substrates in a way that the idea of a future state gains the capability of addressing the muscular system (a *cerebral reflex*; cf. Leff, 1991, 2003).

Laycock's (1845, 1874) idea of cerebral reflexes was adopted and modified by William Carpenter (1852, 1874) who first coined the terms ideo-motor principle and ideo-motor reflex. Like Laycock, Carpenter (1852) described voluntary action as reflex movement that is triggered by "the *anticipation* of a given result being the stimulus which directly and involuntarily prompts the muscular movements that produce it" (p. 153).

Despite these early attempts to ground ideomotor theory in a neuroscientific framework of voluntary action, ideomotor theory did not find its way into contemporary neuroanatomical and neurophysiological approaches (e.g. Haggard, 2008; Wolpert, Ghahramani, & Jordan, 1995; Wolpert & Ghahramani, 2000).[2] These models typically assume a dissociation of action planning and initiation in prefrontal, i.e. non-sensory, cortices on the one hand, and action regulation in parietal cortices on the other hand. Thus, motor commands are hypothesised to be addressed without sensory involvement.

This view is challenged by growing body of evidence for parietal activity prior to movement initiation (e.g. Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Krieghoff, Brass, Prinz, & Waszak, 2009; Sirigu et al., 2004; Soon, Brass, Heinze, & Haynes, 2008). For instance, Soon and colleagues were able to predict a free decision between a left or a right key press from spatial activity patterns in the precuneus (BA 7) several seconds before their participants actually reported a motor intention. Further results from Krieghoff et al. suggest that neural activity in the medial parietal and paramedian cortex reflects a selection between several response alternatives whereas response initiation involves more lateral parietal regions (BA 40).

[2] The lack of neural investigations of ideomotor action is especially puzzling as several studies reported anticipative behavioural control in other non-human vertebrates (e.g. Colwill & Rescorla, 1990) and also in non-vertebrates (Gerber & Hendel, 2006) that might be used as model organisms.

This interpretation is corroborated by findings on increased parietal activity under voluntary action conditions involving a free choice between response alternatives as compared to pure forced choice conditions (Müller et al., 2007). It is further consistent with the generally assumed regulatory role of parietal cortices for action control that has been demonstrated in numerous studies (e.g. Dijkerman et al., 2009; see Haggard, 2008, for an overview).

Furthermore, two studies addressed the neural basis of ideomotor action control directly by adopting the respective designs of experimental psychology (Elsner et al., 2002; Melcher, et al. 2008). Participants of Melcher and colleagues first learned the association of left and right key presses with specific contingent tones. In a following test phase in an fMRI scanner, participants reacted to arbitrary visual target stimuli while either former action effects or new neutral tones were presented as go signals. The presentation of former action effects resulted in increased activity in several brain regions including the supplementary motor area (SMA) and the hippocampus as compared to the presentation of neutral tones. As this activity necessarily reflects backward activation of motor areas through action effects, both brain regions were identified as neural substrates of ideomotor action control.

However, the design of both previous studies on ideomotor action control (Elsner et al., 2002; Melcher et al., 2008) does not directly address the fundamental claim of ideomotor theory, namely that actions are initiated by anticipating their expected or desired outcomes. This gap can be closed with the paradigm introduced in the present Experiment 1 and 2 as the introduced trial-by-trial variation of R-E-compatibility allows the application of neuroimaging methods, especially event-related fMRI. Experiment 3 was designed as a pilot study to adapt the paradigm to suit this enterprise; Experiment 4 then applied the design to event-related fMRI.

5 Experiment 3: Switching Effect Anticipations On and Off Again

Event-related fMRI imposes two constraints on the present experimental design. As first constraint, sensory stimulation and motor activity must be constant across all conditions of the experiment. This condition is already met by the present design as free and forced choice actions involve the same stimuli (except for the respective go-signals) and also involve the same motor response. As second constraint, effect anticipations have to be present in some trials whereas they have to be absent in others to allow a within-subjects analysis of the regional cerebral blood flow (BOLD-signal). This condition is not met by either of the previous experiments: Experiment 1 varied free and forced choices between-subjects and found effect anticipations only for the free choice group whereas Experiment 2 varied free and forced choices within-subjects but found effect anticipations for both choice conditions.

Thus, Experiment 1 suggests that effect anticipations do not occur when participants react exclusively under forced choice conditions. To the contrary, Experiment 2 suggests that effect anticipations are generalized to forced choice actions if a certain proportion of free choice trials are experienced in the same experimental block. Following this line of argument, effect anticipations might occur exclusively for free choice trials when both choice conditions are contained in the same block but free choice trials are relatively rare. I tested this prediction in Experiment 3 by using the same paradigm as in Experiment 2 but only used 33% instead of 50% free choice trials. This proportion seems still relatively high but it was chosen to ensure the maximum possible number of trials for fMRI analysis.

5.1 Method

5.1.1 Participants

Twelve undergraduate students at the University of Würzburg (3 males, 1 left-handed) were recruited and received either course credit or were paid for participation. The mean age was 22.58 years (*SD* = 4.17), participants reported normal or corrected-to normal vision and were naive as to the purpose of the experiment.

5.1.2 Apparatus, Stimuli, and Procedure

Experiment 3 used the same paradigm as Experiments 1 and 2 (**Figure 1**) with the following modifications. Participants experienced free and forced choice trials throughout the experiment with a ratio of 33% and 67%, respectively. The experiment consisted of four training blocks and six test blocks, each of them comprising 63 trials (7 free choice and 14 forced choice trials for each compatibility condition, including 1 deviant effect for each combination of the factors choice and compatibility; training blocks 1-3 again contained only one compatibility condition with tripled trial numbers). No nogo-trials were used.

5.2 Results

As for Experiments 1 and 2, trials with responses prior to the target stimulus or RT < 100 ms (0.6%), response omissions (0.6%), wrong key presses in forced choice trials (2.1%), deviant missings (0.1%), non-simultaneous key presses to deviant effects (1.1%), and key presses in reaction to normal effects (0.4%) were excluded from data analysis (5.0% in total).

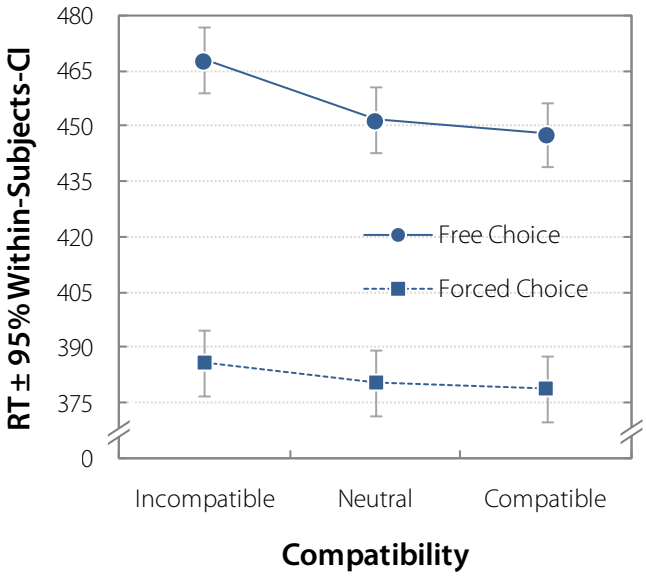

Figure 4. Mean RTs in Experiment 3 as a function of both within-subjects factors, R-E compatibility and choice. Error bars show within-subjects confidence intervals (Loftus & Masson, 1994) that were computed with the aggregated data of all six conditions.

5.2.1 Compatibility effects

A 2 (choice) x 3 (compatibility) within-subjects ANOVA was conducted on the mean RTs of the participants (**Figure 4**) and both, the main effect of compatibility, $F(2, 10) = 10.10$, $p = .004$, $\eta_p^2 = 0.67$, and the main effect of choice, $F(1, 11) = 70.55$, $p < .001$, $\eta_p^2 = 0.87$, were significant. The interaction of both factors only showed a slight tendency, $F(2, 10) = 2.20$, $p = .162$, $\eta_p^2 = 0.31$. However, it approached significance when only testing for its linear component, $F(1, 11) = 4.62$, $p = .055$, $\eta_p^2 = 0.30$, indicating a reduced compatibility effect for forced choice trials (20 ms vs. 7 ms). A direct comparison of compatible and incompatible trials resulted in significantly faster RTs for compatible trials for both choice conditions, with a stronger effect size for free choice trials, $t(11) = 3.38$, $p = .006$, d = 0.99, as compared to forced choice trials, $t(11) = 2.71$, $p = .020$, d = 0.78.

5.2.2 Neutral effects

The impact of neutral effects was assessed by pairwise comparisons with both, compatible and incompatible effects by means of separate two-tailed t-tests. These t-tests were run separately for free and forced choice trials. For both choice conditions, RT in neutral trials differed from RT in incompatible trials; free choice: $t(11) = 2.83$, $p = .016$, d = 0.84; forced choice: $t(11) = 2.35$, $p = .038$, d = 0.69. No significant difference was found between neutral and compatible trials for either choice condition (both p's > .233).

5.3 Discussion

As pilot study, Experiment 3 modified the design of both previous experiments to suit the constraints of event-related fMRI. By using a reduced proportion of free choice trials together with a necessarily increased proportion of forced choice trials, a stronger R-E-compatibility effect resulted for free choice as compared to forced choice trials. Thus, both constraints of event-related fMRI are met: together with balanced sensory stimulation and motor activity, effect anticipations varied within-subjects as a function of free versus forced choice.

These results also extend the findings of Experiment 2 regarding the concept of action control modes (Herwig et al., 2007; Herwig & Waszak, 2009). While participants of Experiment 2 employed an enduring intention-based mode to free and forced choice actions, participants in Experiment 3 employed the intention-based mode only to free choice actions. The corresponding interaction, however, was relatively week and reduced compatibility effects also resulted for forced choice actions. This gradual difference between free and forced choice indicates that the chosen proportion of 33% free choice trials already leads to a partial application of the intention-based mode to

forced choice actions. I still decided to use the design of Experiment 3 without further changes for event-related fMRI to ensure a reliable measurement of neural responses also for free choice trials within a limited scanning time.

6 Experiment 4: Measuring Effect Anticipations with Event-Related fMRI

Experiment 4 took the previously validated design to the fMRI scanner. As the manipulation of free and forced choices is concerned, I expected to replicate the fronto-parietal network that is reliably found in imaging studies of voluntary action (e.g. Krieghoff et al., 2009 Müller et al., 2007;).

Also in accordance with these studies, I hypothesized the neural substrate of ideomotor action to be part of this activated network. To dissect this network into ideomotor and non-ideomotor elements, I planned to use the behavioural R-E compatibility effect of the participants as regressor for the strength of the BOLD signal. As R-E compatibility effects represent a pure measure of effect anticipation (Kunde, 2001, 2003), they should directly correlate with the activity in those neural centres that process effect anticipations.

Taking into consideration that ideomotor effect anticipations are conceptualised to take place in sensory areas, parietal association cortices were my prime region of interest. These areas are not only part of the network subserving voluntary action (Desmurget et al., 2009; Goodale, Milner, Jakobson, & Carey, 1991) but are also specifically involved in the action-related processing of spatially distributed visual information (e.g. Goodale & Milner, 1992; Milner & Goodale, 2006) and spatial working memory (Gruber & von Cramon, 2001, 2003). Furthermore, a huge body of evidence suggests that specifically the left inferior parietal cortex (BA 7 and BA 40) is involved in spatial imagery (Cabeza & Nyberg, 2000; Mazard, Tzourio-Mazoyer, Crivello, Mazoyer, & Mellet, 2004; Mellet, Petit, Mazoyer, Tzourio, 1998, Mellet et al., 2000; Trojano et al., 2004) and movement initiation (Daprati, Sirigu, & Nico, 2010).

6.1 Method

6.1.1 Participants

Eighteen healthy volunteers from the University of Göttingen (7 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 (see **Appendix A**).

6.1.2 Apparatus, Stimuli, and Procedure

Experiment 4 used the same paradigm as its pilot study, Experiments 3. Thus, participants experienced free and forced choice trials throughout the experiment with a ratio of 33% and 67%, respectively. Participants completed the four training blocks at an IBM compatible PC outside the scanner and proceeded immediately with the fMRI session. The scanning session started with a high-resolution anatomical scan, followed by three test runs and each test run was twice as long as a block in Experiment 3 (see **Appendix B**). The participant's head motion was restricted by small cushions.

6.1.3 fMRI Data Acquisition, Preprocessing, and Analysis

Using a 3 T scanner (Siemens Trio, Germany), the fMRI session started with a high-resolution structural scan for each participant (three-dimensional magnetization-prepared rapid-acquisition gradient echo; MP-RAGE). The following functional images comprised thirty-three axial slices of the brain (3 x 3 x 3 mm^3, 20% gap) that were recorded in ascending order parallel to the AC-PC plane.[3] A gradient echo planar

[3] AC = anterior commissure, PC = posterior commissure. For the physical and physiological basis of fMRI, see e. g. Huettel, Song, and McCarthy (2009) or Logothetis, Pauls, Augath, Trinath, and Oeltermann (2001).

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. Three initial dummy volumes were discarded from each session to allow for T1 equilibration effects.

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

The following statistical analyses relied on the general linear model approach of SPM and a vector of temporal onsets for each experimental condition was convolved with a canonical hemodynamic response function (hrf) to produce a predicted hemodynamic response to the respective condition. The to-be modelled conditions resulted from the orthogonal combination of the factors compatibility (compatible vs. incompatible vs. neutral), choice (free vs. forced) and response (left vs. right) and trials with deviant effects or errors were modelled separately but were not included in further analyses (see **Appendix C** for details on the model).

To assess the impact of free choices compared to forced choices, I constructed a linear t contrast across all conditions (*Free vs. Forced* hereafter) and an additional contrast for each response side (for validating the regression analysis). Contrast images were thresholded at $p < .050$ and controlled for the family-wise error (FWE-correction; see e.g. Bennett, Wolford, & Miller, 2009) with a minimum cluster size of 15 contiguously active voxels.

Finally, to identify the regions responsible for ideomotor action control within the contrast Free vs. Forced, I performed a regression analysis with the behavioural R-E compatibility effect for each participant ($RT_{incompatible/free}$ - $RT_{compatible/free}$). The regression was computed as a single-step whole-brain analysis so that the signal change was correlated with the behavioural effect for each voxel. This analysis was thresholded at $p < .005$, uncorrected, with a minimum cluster size of 15 voxels (cf. Formann et al., 1995).[4]

6.2 Behavioural Results

As for the three previous experiments, 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). Furthermore, to make the behavioural analysis similar to fMRI analysis, all trials with deviant effects were excluded.

6.2.1 Compatibility effects

In a 2 (choice) x 3 (compatibility) within-subjects ANOVA on the mean RTs of the participants (**Figure 5**), the main effect of compatibility, $F(2, 16) = 12.58$, $p < .001$, $\eta_p^2 = 0.61$, and the main effect of choice, $F(1, 17) = 142.36$, $p < .001$, $\eta_p^2 = 0.89$, were both significant. Furthermore, a significant interaction, $F(2, 16) = 3.74$, $p = .047$, $\eta_p^2 = 0.32$, indicated a stronger compatibility effect for free choice. Accordingly, direct comparisons of compatible and incompatible trials resulted in significantly faster RTs for compatible trials for free choice actions, $t(17) = 3.55$, $p = .002$, d = 0.84, whereas only a marginally significant difference was present for forced choice, $t(17) = 1.99$, $p = .062$, d = 0.47.

[4] The present data set allows a variety of additional informative analyses, such as pairwise comparisons of compatibility conditions with interaction contrasts, psychophysiologic interactions (PPIs) or dynamic causal modeling (DCM). These analyses, however, go beyond the scope of the present manuscript and may be presented at a different point.

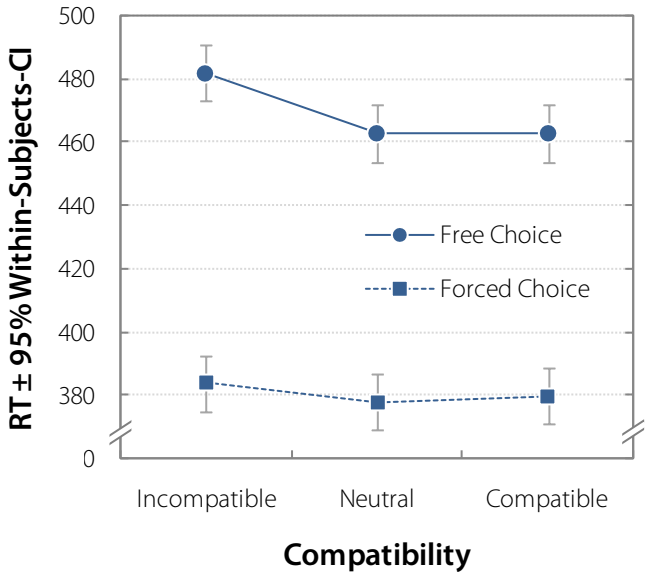

Figure 5. Mean RTs in Experiment 4 as a function of both within-subjects factors, R-E compatibility and choice. Error bars show within-subjects confidence intervals (Loftus & Masson, 1994) that were computed with the aggregated data of all six conditions.

6.2.2 Neutral effects

The impact of neutral effects was assessed by pairwise comparisons with both, compatible and incompatible effects by means of separate two-tailed t-tests. As for Experiment 3, these t-tests were run separately for free and forced choice trials. For both choice conditions, RT in neutral trials differed from RT in incompatible trials; free choice: $t(17) = 3.99$, $p < .001$, d = 0.94; forced choice: $t(17) = 3.37$, $p = .004$, d = 0.79. No significant difference was found between neutral and compatible trials for either choice condition (both p's > .262).

6.3 fMRI Findings: Free Choice vs. Forced Choice

The contrast Free vs. Forced revealed a pronounced fronto-parietal network including bilateral activations of the dorso-lateral prefrontal cortex (DLPFC), structures of the fronto-medial wall, insular cortex as well as lateral parietal regions (see **Table 1** and **Figure 6**). Further regions that were only activated at a lowered statistical threshold comprised the medial parietal cortex, the basal ganglia, and the cerebellum; see also **Appendix D** for tabular results and **Appendix E** for an interactive 3D model (digital version only).

Table 1. Anatomical location, cluster size, MNI-coordinates, and peak statistics for the contrast Free vs. Forced, thresholded at $p < .050$, FWE-corrected, with a minimum cluster size of $k = 15$ contiguous voxels. Results for a lowered threshold of $p < .001$, uncorrected, and $k = 10$ can be found in **Appendix D**.

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.

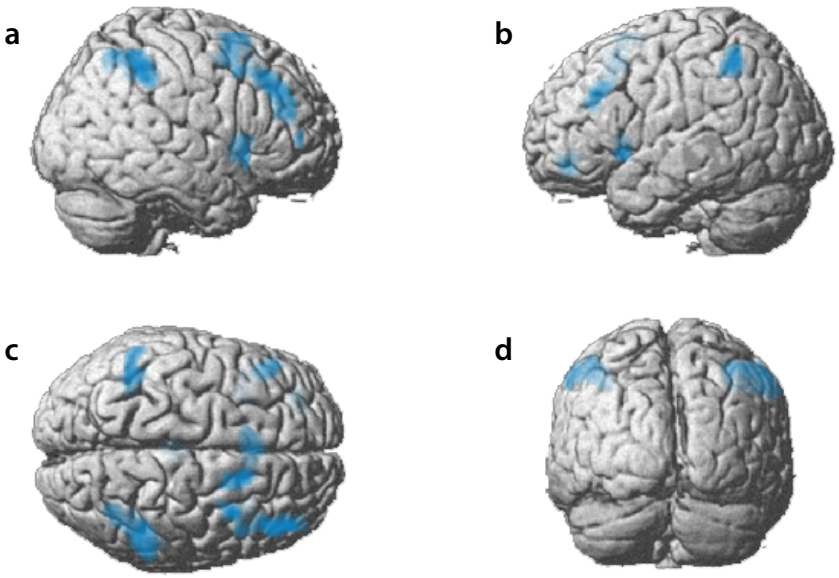

Figure 6. Fronto-parietal networt subserving the control of freely chosen actions (contrast Free vs. Forced thresholded at $p < .050$, FWE-corrected, and minimum cluster size of $k = 15$). From left to right: **(a)** inferior parietal lobule (BA 40), DLPFC, and insula; **(b)** orbitofrontal cortex, DLPFC, insula, and inferior parietal lobule (BA 40); **(c)** inferior parietal lobule, fronto-median wall, and DLPFC; **(d)** inferior parietal lobule (BA 40). See also **Appendix E** for an interactive 3D model of this contrast (digital version only).

6.4 Correlating Compatibility Effects and BOLD-Response

Regression analysis revealed circumscribed activations of motor areas on both, the left superior and the left middle frontal gyrus (BA's 6 and 8, respectively), bilateral parahippocampal clusters as well as a large cluster within the inferior parietal lobe (BA 40; see also **Figure 7** and **Table 2**). Additionally, increased activity was present in the right temporo-parietal junction, partly extending to the right superior temporal gyrus (BA 22).

In order to critically assess the reported correlations, two more conservative approaches are presented in **Appendix F**. Both approaches replicated the findings of the original regression analysis.

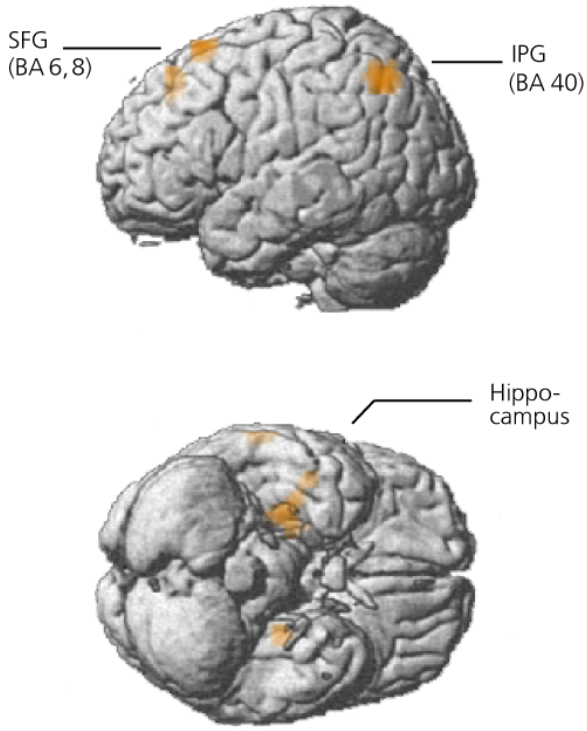

Figure 7. Correlation of behavioural R-E-compatibility effects with the signal strength in the main contrast (Free vs. Forced), thresholded at $p < .005$, uncorrected, with a minimum cluster size of $k = 15$ voxels. Even though the chosen statistical threshold, together with a cluster size of $k \geq 10$, provides a reliable criterion (e.g. Formann et al., 1995), the results were extensively validated to ensure maximal reliability (see **Appendix F** for details).

Table 2. Anatomical location, cluster size, MNI-coordinates, and peak statistics for the regression analysis with behavioural R-E-compatibility effects within the contrast Free vs. Forced, thresholded at $p < .005$, uncorrected, with a minimum cluster size of $k = 15$ contiguous voxels.

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	L	15	-27	-22	-23	3.70	3.10
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.

7 Discussion: The Neural Basis of Ideomotor Effect Anticipations

Experiment 3 and 4 investigated the neural basis of ideomotor effect anticipations by combining the present behavioural paradigm (see **Figure 1**) with fMRI recording. In a setting where a behavioural R-E compatibility effect was present for free choice actions but not for forced choice actions, I first contrasted free and forced choice actions and identified the neural correlate of ideomotor action control by using the behavioural effects as regressors within this contrast. The comparison of free and forced choice actions replicated the robust fronto-parietal network for voluntary actions (e.g. Haggard, 2008; Krieghoff et al., 2009; Müller et al., 2007) while regression analysis identified the hippocampal formation, the left inferior parietal lobule (BA 40) as well as left prefrontal motor areas (BA 6, BA 8) as central structures for ideomotor action control. I will first focus on the implications of the reported frontal and parietal regions and the laterality that is suggested by the present results. Then, I will integrate the present findings in the body of literature on the neural basis of action control.

7.1 Ideomotor Effect Anticipations in the Parietal Lobe?

Prior studies on ideomotor processes used a considerably different approach as the present study by presenting learned action effects to observe a backward activation of (ideo)motor areas (Elsner et al., 2002; Melcher et al., 2008). These studies reported activity of the hippocampus as well as frontal motor areas, more specifically the supplementary motor area (SMA) and the dorsal premotor cortex. The present results are consistent with these investigations concerning the involvement of hippocampal and

(pre)frontal motor areas. Presumably, the hippocampus plays a central role in activating learned R-E associations while the resulting motor plan is generated in frontal areas.

However, as noted before, these studies did not address effect anticipations directly. Consistent with the classic ideomotor assumption that effect anticipations are performed by those brain areas that process the effects afterwards, I found additional activation in the left inferior parietal lobule (BA 40) that extended into more posterior regions such as the angular gyrus (BA 39). Activity in this region presumable reflects anticipative processes. I will first give a general overview of evidence supporting the claim that parietal activity might represent spatial anticipations and will then focus on the laterality suggested by the present results.

The interpretation of parietal (BA 40) activity reflecting the anticipation of spatially distributed action effects is consistent with recent studies on human spatial working memory such as the experiments of Gruber and von Cramon (2001, 2003) that indicate a neuroanatomical dissociation of verbal and visuospatial working memory. Most importantly, these studies found consistent activation of inferior parietal networks when participants maintained a representation of spatially distributed stimuli in their working memory (the position of several items in a 5 x 5 matrix). Because maintaining a spatial representation arguably reflects similar processes as anticipating a spatial action effect, these results support my interpretation of parietal activity reflecting anticipative processes.

This interpretation is also consistent with studies on mental imagery that found the inferior parietal lobe, most prominently the BA 40, to be involved in creating a mental representation of spatially distributed stimuli (Cabeza & Nyberg, 2000; Mazard et al., 2004; Mellet, et al., 1998, 2000; Trojano et al., 2004). The comprehensive review of

Cabeza and Nyberg (2000) for instance reports bilateral involvement of several lateral parietal regions in the perception of such stimuli (BA's 7, 39, and 40). Most strikingly, this review also found especially the left hemispheric parts of these regions to be involved in spatial imagery. The specific contribution of left but not right parietal regions to mental imagery is also consistent with the present findings because only activity in the left inferior parietal lobule correlated with the behavioural R-E compatibility effect.

This view is further supported by studies that specifically addressed laterality differences in the parietal lobes (for a review see Daprati et al., 2010). For instance, lesions of the left parietal lobe impair the patient's ability to plan and execute complex gestures and object-related actions (ideomotor apraxia; Buxbaum, Kyle, Grossmann & Coslett, 2007; Daprati et al., 2010; Leiguarda & Marsden, 2000; Wheaton & Hallett, 2007). Furthermore, recent neuropsychological models proposed a critical role of parieto-frontal connections in the left hemisphere as well as projections to the basal ganglia for the deficits observed in patients with left parietal lesions (Buxbaum et al., 2007; Gross & Grossmann, 2008; Goldenberg, 2009; Goldenberg & Spatt, 2009).[5] These models assume that the left inferior parietal lobule hosts a gesture memory system as well as representations of external action-relevant objects – a notion that is supported by recent findings on predominantly left parietal activity in object-targeted actions in healthy participants irrespective of the hand used (Bohlhalter et al., 2009; Gut et al., 2007; Moll et al., 2000).

[5] It is interesting to note that the first comprehensive account of apraxia by Hugo Liepmann (1905, 1908) already focused on the specific contribution of the left inferior parietal lobule to movement initiation and regulation (**Figure 8**; see also Goldenberg, 2003).

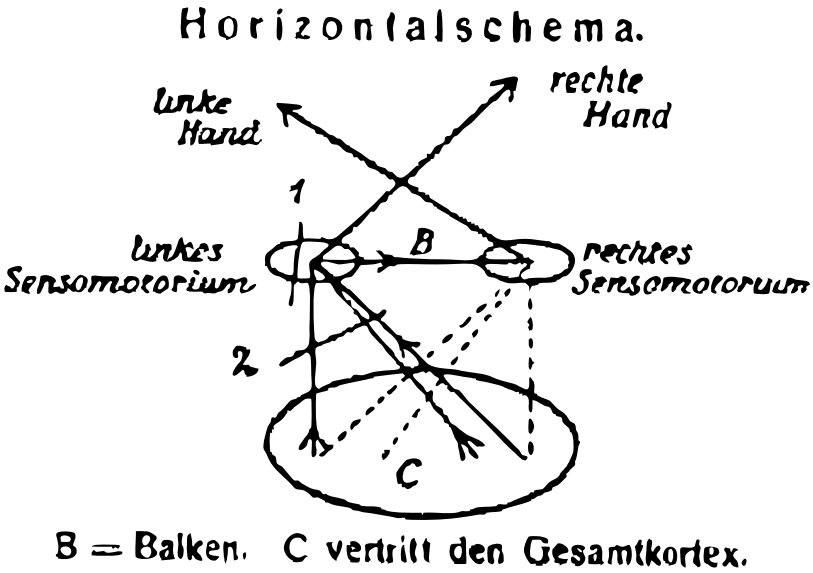

Figure 8. Liepmann's (1908) classical model of ideomotor apraxia assuming a dominant role of the left inferior parietal lobule for initiation and regulation of actions (reproduced after Goldenberg, 2009). "Movement formulas" are created in the entire cerebral cortex (C) and the forwarded to sensorimotor regions in the left inferior parietal lobe (1). This area controls the right hand or, via projections to the right hemisphere (B = corpus callosum), eventually also the left hand.

Moreover, a particularly interesting study on patients with left parietal damage (centred on BA 40) suggests that this region is also responsible for generating a forward model of own movements (Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999). Sirigu and colleagues asked those patients to perform simple versus complex finger movements while the visual feedback of the movements was altered systematically. The patients either saw their own or the experimenter's hand on a monitor and judged whether the hand was their own or not. When the experimenter performed a different movement, patients correctly identified the hand as alien. But when the experimenter performed the same movement as the patient, their judgements were less accurate than those of healthy controls and controls with non-parietal lesions. This was also true if the patients failed to execute the movement correctly, suggesting that the parietal lobe

monitors and compares expected interoceptive and overt exteroceptive consequences of a movement (see also Daprati & Sirigu, 2005; Daprati, Wriessnegger, & Lacquaniti, 2007; Fink et al. 1999; Sirigu et al., 1996). This forward model implies the usage of R-E associations so that the reverse process of ideomotor effect anticipations is also likely to rely on left parietal areas.

To sum up, neuropsychological studies as well as experiments on mental imagery and working memory suggest a predominant role of the left inferior parietal cortex for the generation of mental representations of spatial information as well as the transformation of such information into overt movement. These findings strongly support my present interpretation: ideomotor effect anticipations seem to be based on left inferior parietal regions, most possibly BA 40.

7.2 Plausibility of Further Activations

Besides the prominent activation of the left BA 40, **Table 2** also lists several other activation foci that correlated with the behavioural R-E compatibility effect. As described above, the observed prefrontal and (para-)hippocampal activation is highly consistent with prior investigations on ideomotor processes (Elsner et al., 2002; Melcher et al., 2008).

Additionally, **Table 2** lists a prominent cluster of temporal activation, extending from the right superior temporal sulcus (BA 22) to the temporo-parietal junction (TPJ). This area is crucial for spatial awareness as put forward by investigations of spatial neglect in humans (Karnath, Ferber, & Himmelbach, 2001) and non-human primates (Watson, Valenstein, Day, & Heilman, 1994). For instance, intriguing results from the study of Karnath and colleagues (2001) suggest that lesions of the superior temporal cortex (BA's 22 and 42) are responsible for spatial neglect.

Thus, while the left superior temporal cortex, hosting Wernicke's area, is crucial for speech perception (e.g. Binder et al., 2000), its right equivalent seems to generate spatial awareness for both visual fields. The observed correlation of the R-E compatibility effect with superior temporal areas might thus reflect increased awareness of the spatial action effects (possibly in combination with body awareness as suggested by Tsakiris, Constantini, & Haggard, 2008, regarding activity in the right TPJ).

7.3 Limitations of the Present Study

Even though the present approach identified circumscribed areas subserving ideomotor action control, it has several limitations that arise from two methodological aspects: the constant visual stimulation in all conditions of the behavioural task as well as inherent limitations of functional MRI, especially regarding its temporal resolution.

Constant visual stimulation and motor activity for free and forced choice actions were necessary prerequisites to avoid confounding ideomotor processes with basal visual or motor processes. Thus, it enabled us to address ideomotor effect anticipations directly with regard to their function in action control. However, a constant visual stimulation also implies that anticipations of specific properties of action effects (such as colour or shape) cannot be identified in the fMRI signal because the same activations will be elicited by the perception of these effects. In turn, ideomotor effect anticipations might involve further, effect specific areas that were not found with the present design. This speculation is supported by findings on common neural circuits for perception and imagination of specific stimuli (e.g. O'Craven & Kanwisher, 2000).

A second limitation of the present study is the limited temporal resolution of fMRI. Accordingly, the present experiment does not address the temporal dynamics of ideomotor effect anticipations – an enterprise that is worthwhile to be performed in

future studies. Combining electroencephalography (EEG), providing optimal temporal resolution, with other imaging techniques such as fMRI or near-infrared spectroscopy (NIRS) seems to be a promising account, especially regarding fronto-parietal interactions during action initiation and execution (Karch et al., in press; cf. Brass et al., 2005, for related findings on cognitive control). The present behavioural paradigm provides a suitable setting for such multimodal assessments of ideomotor action. A second possibility to assess the temporal dynamics of action control would be separating several aspects of voluntary action experimentally – for instance by dissociating action planning and execution by delaying the start signal of an action (Krieghoff et al., 2009). This latter design would overcome the limited temporal resolution of fMRI even without using further neurophysiological techniques.

A final limitation of the present study is the purely right-handed sample of participants. Thus, it does not speak to the neural architecture of ideomotor processes for the approximately 10% left-handed people that exhibit manifest differences to right-handed controls in several motor-related tasks (e.g. Daprati & Sirigu, 2005; Gut et al., 2007; Kawashima, Inoue, Sato, Fukuda, 1997; Kim et al., 1993; Pollok, Gross, & Schnitzler, 2006; Willems, Toni, Hagoort, & Casasanto, 2009). For instance, a recent study on motor imagery (Willems et al., 2009) showed predominantly right-hemispheric activation during motor imagining of left-handed participants and predominantly left-hemispheric activation for right-handed participants (see Maruff et al., 1999, for related findings). In the light of these findings, ideomotor action control is likely to differ between right- and left-handers, too, so that the present results do not generalise to the left-handed population.

7.4 Integrating Ideomotor Theory in Neural Models of Action Control

The two most prominent regions identified as neural correlates of ideomotor effect anticipation, the left inferior parietal lobule (BA 40) and left prefrontal motor areas (BA's 6 and 8), are anatomically as well as functionally integrated in a vast front-parietal network that is commonly associated with voluntary action (Haggard, 2008). The huge body of literature on voluntary action allows a detailed integration of these areas in a wider framework.[6]

In this framework, the interplay of prefrontal motor areas and inferior parietal regions most likely creates and executes motor programs (e.g. Andersen & Cui, 2009; Haggard, 2008; Müller et al., 2007; Pesaran, Nelson, & Andersen, 2008). For instance, Pesaran and colleagues investigated the neural activity during a manual exploration task of two macaque monkeys. The monkeys serially reached to three targets and could either choose the order or had to follow an imperative sequence. Comparing free and forced choice conditions, Pesaran et al. found enhanced activity in the dorsal premotor area and the macaque parietal reach region, suggesting that these regions transform behavioural goals and decisions into movement plans. An fMRI study on parietal activity during a delay phase between movement planning and initiation pointed towards a similar function of the posterior parietal cortex in humans (Connolly, Andersen, &

[6] Given the immense body of literature on human action, the present discussion concentrates only on a limited proportion of the available evidence. Further fascinating fields of research that were deliberately omitted include decision making with regard to voluntary action, action conflict, visually guided actions and the integration of feedback in action control, the development of action control, or task-set specific aspects of action control. Comprehensive reviews on these topics are provided by Jeannerod (1997), Morsella, Bargh, and Gollwitzer (2008), and Rosenbaum (2009).

Goodale, 2003; see also Culham & Kanwisher, 2001, for a discussion on the homology of the parietal cortices of humans and monkeys).

In addition to these parieto-frontal circuits, several studies relate the (anterior) insular cortex to body schemata (Baier & Karnath, 2008; Craig, 2002, 2009), sense of agency (Farrer & Frith, 2002; Farrer et al., 2003; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), and sensorimotor functions such as forming A-E associations (Mutschler et al., 2007). Furthermore, these functions seem to be based on different parts of the anterior insula (Mutschler et al., 2009) and rely, at least partly, on interactions between the anterior insular and right posterior parietal regions (Daprati et al., 2010; Farrer et al., 2003; Fink et al., 1999; Kammers et al., 2009). These latter studies also point towards an important direction for future research on ideomotor action control: having isolated several regions for ideomotor effect anticipations, it is now possible to address the functional connectivity of these regions (see Westendorff, Klaes, & Gail, 2010, for a promising account).

Taken together, the present results integrate perfectly in the present literature on voluntary action – indicating a functional specialisation of left-hemispheric frontal and parietal regions for movement planning and right-hemispheric regions for perceiving action effects and inferring sense of agency. Finally, recent theoretical accounts proposed a broader view on the discussed fronto-parietal networks. Naghavi and Nyberg (2005) for instance describe a model that relates the network to a multitude of cognitive functions such as attention, memory, and consciousness. Relating research on the fundamental processes of voluntary action to these higher order cognitive functions is a fascinating challenge in the future study of action control in general and research on ideomotor processes in particular.

The present results are a promising first step in this direction, or, to use the words of William B. Carpenter (1852, p. 153): "Thus the *ideo-motor* principle of action finds its appropriate place in the physiological scale, which would, indeed, be incomplete without it."

CONCLUDING REMARKS

In accordance with Johann Friedrich Herbart's (1825) classical advice to investigate ideomotor action with psychological as well as physiological methods, I set out to fill two important empirical gaps. Experiment 1 and 2 found comprehensive evidence for ideomotor effect anticipations under rapidly-varying R-E relations, thus extending empirical evidence for ideomotor action control to these more ecologically valid settings. Based on the same paradigm, Experiment 3 and 4 concentrated on the physiological aspect of ideomotor action control and investigated ideomotor effect anticipations with event-related fMRI.

The present results add to our increasing understanding of voluntary action and thus, in more general terms, the empirical search for a solution of the ancient mind-body problem. The present study also points out a way to integrate behavioural and neurophysiological methods in a synergetic way. A strategy that might be used fruitfully by all the different scientific disciplines working on the mind-body problem, be it the basic approach of philosophy, psychology, and neuroscience, or the applied approach of robotics and medicine.

APPENDICES

Appendix A: Informed Consent Form

Georg-August-Universität Göttingen
Zentrum 16: Psychosoziale Medizin

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Probandeninformation

Ausführen motorischer Handlungen und Überwachung deren Konsequenzen

Liebe Studienteilnehmerin, lieber Studienteilnehmer!

Wir möchten Sie herzlich einladen, an einer wissenschaftlichen Studie teilzunehmen. Als Universitätsklinik führen wir neben der Behandlung von Patienten auch wissenschaftliche Untersuchungen durch, die das Ziel haben, grundlegende Erkenntnisse über die Funktionen des gesunden Gehirns zu erwerben. Hierzu sind wir auf Ihre aktive Mitarbeit als Proband angewiesen, da wir nur so die neuronalen Mechanismen der Handlungskontrolle genauer verstehen können.

1. Wissenschaftlicher Hintergrund
Eine zentrale Fähigkeit des gesunden menschlichen Gehirns besteht darin, schnell und präzise diejenigen motorischen Handlungen bzw. Bewegungen auswählen und initiieren zu können, die uns zu einem gegebenen Verhaltensziel führen. Dabei kann es sich um das einfache Öffnen einer Tür durch den gezielten Griff zum Türknauf, bis hin zum Spielen eines Musikstückes durch die feinmotorische Betätigung einer Klaviertastatur oder das Lenken eines Autos handeln. Gegenstand der vorliegenden Studie sind die neuronalen Mechanismen, die der Auswahl und Initiierung motorischer Handlungen zugrunde liegen. Genauer gesagt möchten wir untersuchen, welche Hirnareale an der Generierung motorischer Willkürbewegungen beteiligt sind bzw. diese ermöglichen.

2. Grund für die Durchführung der Studie
Veränderungen im beobachtbaren Verhalten bei psychiatrischen Patienten können auf eine gestörte Funktion der an den beschriebenen Denk- bzw. Steuerprozessen beteiligten neuronalen Systeme zurückzuführen sein. Das Wissen um solche (neuro-)funktionellen Störungen kann wesentlich zum besseren Verständnis betreffender Erkrankungen beitragen und außerdem wichtige Implikationen für deren medikamentöse oder psychotherapeutische Behandlung haben. Eine genaue Bestimmung der Art und Richtung von krankheitsbezogenen Abweichungen oder Störungen ist nur möglich, wenn genaue Kenntnisse über Funktionsweise des gesunden Gehirns vorliegen. Daher führen wir eine Studie durch, die die Steuerung von motorischen Bewegungen unter verschiedenen experimentellen Bedingungen bei gesunden (Normal-)Probanden untersucht.

Für eine ausführliche Erläuterung der Ziele dieser Untersuchung steht Ihnen der Versuchleiter bzw. die Versuchsleiterin nach dem Ende Messung sehr gerne zur Verfügung.

3. Studiendurchführung
Die Untersuchung besteht aus zwei Teilen:

1. Training: Hierbei werden Sie zunächst an einem handelsüblichen PC ein kurzes Experiment durchführen (Dauer: ca. 15 Min.), bei dem Sie auf Pfeilrichtungen per Tastendruck reagieren. Dabei handelt es sich um die gleiche Aufgabe, die Sie später auch im Kernspintomographen ausführen werden. Durch das Training soll gewährleistet werden, dass Sie die Aufgabe im Kernspintomographen möglichst fehlerfrei ausführen können.
2. fMRT: Anschließend werden Sie die gleiche Aufgabe im „Kernspintomographen“ durchführen. Dabei handelt es sich um eine medizinisch-technische Apparatur, die zur bildgebenden Untersuchung des Gehirns angewendet wird. Durch die Magnet-Resonanz-Tomographie – auch „Kernspintomographie“ genannt – werden Schichtaufnahmen des Gehirns anfertigt. Mit einer speziellen Technik lässt sich vereinfacht gesagt der Sauerstoffverbrauch einzelner

Hirnstrukturen messen und damit auf deren Aktivität und Funktionalität schließen. Die kernspintomographische Untersuchung ist völlig schmerzfrei und ohne jede Strahlenbelastung, da diese Technik mit Magnetfeldern arbeitet. Nach heutigem Wissensstand, basierend auf mehrjährigen Erfahrungen mit der MRT-Technologie, sind keine Nebeneffekte zu erwarten. Die Untersuchung dauert etwa 50 Minuten. Die Anwendung von Magnetfeldern schließt die Untersuchung von Personen aus, die elektrische Geräte (z. B. Herzschrittmacher, Medikamentenpumpen usw.) oder Metallteile (z. B. Schrauben nach Knochenbruch) im oder am Körper tragen. Hierzu werden sie noch einmal gesondert informiert und befragt.

4. Magnetresonanz-Tomografie und Spektroskopie

Die erfolgreiche Behandlung einer Erkrankung bedingt eine genaue Diagnose und Beobachtung der therapeutischen Maßnahmen. Die Magnetresonanz-Tomografie (MRT, auch: Kernspin-Tomografie) und Spektroskopie (MRS) bieten hierzu neue Möglichkeiten, die mit anderen Methoden nicht zu erhalten sind. Obwohl das Verfahren bereits eine große klinische Verbreitung gefunden hat, ist weiterhin eine umfangreiche Forschung erforderlich, um neue Methoden und Anwendungsbereiche zu erschließen. Dies gilt insbesondere für neue Wege, das menschliche Gehirn zu untersuchen.

Es werden keine Röntgenstrahlen oder radioaktiven Stoffe verwendet.

Während der Untersuchung befindet sich Ihr Körper in einem Magnetfeld. Radiowellenimpulse mit UKW-Frequenzen erzeugen Echosignale, die von empfindlichen Antennen aufgefangen werden. Ein Computer errechnet hieraus Schnittbilder Ihres Körpers.

Nach Einführung der MRT vor etwa 20 Jahren werden heutzutage jährlich etwa 60 Millionen Untersuchungen weltweit durchgeführt. Dabei haben sich keine nachteiligen Neben- oder Nachwirkungen gezeigt. Nach dem Stand unseres Wissens sind bei den von uns verwendeten Bedingungen keine schädigenden Wirkungen zu erwarten.

Bitte fragen Sie uns, wenn Sie etwas nicht verstanden haben oder wenn Sie mehr über die Untersuchungsmethode erfahren wollen. Wir geben Ihnen gerne weitere Auskunft im Gespräch. Bitte fragen Sie nach allem, was Ihnen wichtig erscheint.

4.1 Die Untersuchung

Die Untersuchung wird in einem speziellen Raum durchgeführt, um Störungen durch lokale Rundfunksender zu vermeiden. Sie liegen auf einer Liege, die sich in eine etwa 65 cm große Öffnung des Gerätes bewegt. Je nach Fragestellung beträgt die Untersuchungszeit eine halbe bis zwei Stunden. Sie werden allerdings nur dann untersucht, wenn sie das typische funktionsbedingte Klopfen hören, das durch das Zuschalten schwacher Magnetfelder verursacht wird. Von der Untersuchung selbst ist im Normalfall nichts zu spüren. Bei bestimmten Untersuchungen können in seltenen Fällen Nerven stimuliert werden, was zu einem leichten „Kribbeln“ oder Zucken von Muskeln während der Messung führen kann, aber keinerlei Gefahr für Sie darstellt.
Sie sollten ruhig und entspannt liegen, sich während der Untersuchung nicht bewegen und insbesondere den Kopf ruhig halten. Über eine Notfallklingel und eine Gegensprechanlage können Sie jederzeit mit dem Untersucher, der Sie auch sehen kann, Kontakt aufnehmen. Nach Möglichkeit sollten Sie hierfür aber eine Pause zwischen den Messungen abwarten.

4.2 Sicherheit

Bevor Sie den Untersuchungsraum betreten, ist es unbedingt notwendig, alle metallischen Gegenstände abzulegen, die sich an Ihrem Körper, an Ihrer Kleidung, oder in Ihren Taschen befinden (z.B. Mobiltelefone, Münzen, Kugelschreiber, Schlüssel, Haarspangen, Uhren, Schmuck, Brillen, Gürtel, Hörgeräte). Bitte beachten Sie auch, dass Scheckkarten mit Magnetstreifen außerhalb des Untersuchungsraumes bleiben müssen. Sie werden sonst im Magnetfeld gelöscht.
Die Untersuchung selbst ist ein völlig ungefährliches Verfahren. Für gewisse Risikogruppen, z.B. Personen mit Metallteilen im Körper (Implantaten), mit stark angegriffenem Herz-Kreislaufsystem oder unter dem Einfluss bestimmter Medikamente, birgt sie jedoch z. T. erhebliche Gefahren. So können beispielsweise im Magnetfeld Knochenschrauben verdreht, Gefäßclips gelöst werden oder eine Überlastung des Herz-Kreislaufsystems auftreten. Damit wir eine Gefährdung für Sie ausschließen können, erhalten Sie von uns einen Fragebogen, den Sie bitte gründlich durchlesen und gewissenhaft ausfüllen.

5. Risiken und Nebenwirkungen, Versicherung

Risiken der Magnetresonanztomographie sind bei Beachtung der Ausschlusskriterien und Vorsichtsmaßnahmen nicht bekannt.

Für das vorliegende Projekt ist der Abschluss einer gesetzlichen Probandenversicherung nicht notwendig, da keinerlei spezifische Risiken bestehen.

6. Die wichtigsten Aspekte am Schluss noch einmal in Stichworten

- Die Teilnahme an dieser Studie ist freiwillig.
- Diese Studie dient nicht der medizinischen Diagnostik.
- Sie können jederzeit ohne Angabe von Gründen aus der Studie ausscheiden bzw. den Abbruch einer laufenden Messung verlangen.
- Durch ein Ablehnen oder einen Abbruch der Studie haben Sie keinerlei Nachteile zu erwarten.

Ihre personenbezogenen Daten werden gespeichert und verarbeitet. Zum Schutz dieser Daten sind organisatorische Maßnahmen getroffen, die eine unbefugte Weitergabe an Dritte verhindern. Für die wissenschaftliche Auswertung werden Ihre persönlichen Angaben anonymisiert, d. h. ohne Ihren Namen und das Geburtsdatum ausgewertet.

Die im Zuge der durchgeführten Untersuchung generierten strukturellen Hirnbilder werden routinemäßig von einem Neuroradiologen durchgesehen. „Wir gehen davon aus, dass Sie informiert werden wollen, wenn einbehandlungsbedürftiger Zufallsbefund im Laufe der Studie festgestellt werden sollte. Sofern Sie damit nicht einverstanden sind, möchten wir Sie bitten, an der vorliegenden Studie nicht teilzunehmen.

Name und Adresse des Prüfarztes

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Telefon: 0551-39-66-10/11

Geburtsdatum: Gewicht:

Anschrift: Medikamente:

Telefon:

Beruf:

---------- wird vom Personal ausgefüllt ----------

Bemerkungen:.....

.....

.....

Datum:.....Unterschrift:.....

Einverständniserklärung zur Studienteilnahme und Magnetresonanz-Untersuchung

MR-Forschung in der Neurologie und Psychiatrie

Bereich Humanmedizin - Georg-August-Universität Göttingen

Name: _____

Geburtsdatum: _____

Das Original dieser Einwilligungserklärung verbleibt bei den Unterlagen. Eine Kopie der Einwilligungserklärung wird dem Probanden ausgehändigt.

Ich _____

erkläre, dass ich die Probandeninformation zur wissenschaftlichen Untersuchung:

Ausführen motorischer Handlungen und Überwachung deren Konsequenzen

und diese Einwilligungserklärung erhalten habe.

Ich wurde von einem Mitarbeiter der Forschergruppe „MR-Forschung in der Neurologie und Psychiatrie“ vollständig über Wesen, Bedeutung und Tragweite der Magnetresonanz-Untersuchung aufgeklärt. Ich habe den Aufklärungstext gelesen und verstanden. Ich hatte die Möglichkeit, Fragen zu stellen, und habe die Antworten verstanden und akzeptiere sie. Ein Mitarbeiter der Forschergruppe „MR-Forschung in der Neurologie und Psychiatrie“ hat mich über die mit der Teilnahme an der Untersuchung verbundenen Risiken und den möglichen Nutzen informiert.

Ich hatte ausreichend Zeit, mich zur Teilnahme an dieser Untersuchung zu entscheiden und weiß, dass die Teilnahme **freiwillig** ist. Ich weiß, dass ich jederzeit und ohne Angaben von Gründen diese Zustimmung widerrufen kann, ohne dass sich dieser Entschluss nachteilig auf eventuell spätere ärztliche Behandlungen auswirken wird.

Mir ist bekannt, dass meine persönlichen Daten in verschlüsselter Form gespeichert werden. Ich erkläre mich damit einverstanden, dass die im Rahmen der Magnetresonanz-Untersuchung von mir erhobenen Daten für die Entwicklung und Anwendung von Verfahren in der biomedizinischen Forschung genutzt und verarbeitet werden dürfen. Mir ist bekannt, dass mein Name, mein Geburtsdatum, mein Gewicht, mein Geschlecht, meine Telefonnummer und meine Adresse in einer Kartei der MR-Forschergruppe der Georg-August-Universität Göttingen gespeichert werden. Die Messdaten werden getrennt hiervon aufbewahrt. Ihre Verwendung erfolgt in namentlich nicht kenntlicher Form.

In diesem Zusammenhang möchten wir darauf hinweisen, dass die im Zuge der Testung erhobenen Daten keinerlei medizinische Diagnosen erlauben, d.h. mit dieser Testung können Krankheiten weder gesucht noch ausgeschlossen werden.
Mir ist bekannt, dass ich Auskunft über die gespeicherten Daten erhalten kann, und dass ich mein Einverständnis zur Speicherung der personenbezogenen Daten jederzeit widerrufen kann. Im Falle des Widerrufs werden alle gespeicherten personenbezogenen Daten gelöscht.

Auf Wunsch erhalte ich eine Kopie des Informationsblattes und dieser Einwilligungserklärung. Ich erkläre hiermit meine freiwillige Teilnahme an dieser Untersuchung.

☐ Ich wurde für mich ausreichend mündlich und schriftlich über die wissenschaftliche Untersuchung informiert.

☐ Ich weiß, dass ich jederzeit meine Einwilligung, ohne Angaben von Gründen, widerrufen kann, ohne dass dies für mich nachteilige Folgen hat.

☐ Ich bin damit einverstanden, dass die im Rahmen der wissenschaftlichen Untersuchung über mich erhobenen Daten sowie meine sonstigen mit dieser Untersuchung zusammenhängenden personenbezogenen Daten aufgezeichnet werden. Es wird gewährleistet, dass meine personenbezogenen Daten nicht an Dritte weitergegeben werden. Bei der Veröffentlichung in einer wissenschaftlichen Zeitung wird aus den Daten nicht hervorgehen, wer an dieser Untersuchung teilgenommen hat. Meine persönlichen Daten unterliegen dem Datenschutzgesetz.

☐ Mit der vorstehend geschilderten Vorgehensweise bin ich einverstanden und bestätige dies mit meiner Unterschrift.

_____ den, _____ _____

(Ort) (Datum) (Proband)

_____ den, _____ _____

(Ort) (Datum) (Prüfarzt/ Studienleiter)

Appendix B: Trial Numbers During fMRI Scanning

Table A1. Trials by condition in Experiment 4. The trial sequence was controlled for all possible dependencies at trial n-1 and was generated with CORE (Pfister, 2009).

Choice	Compatibility	Run 1		Run 2		Run 3		Σ	
		N	D	N	D	N	D	N	D
Free	Compatible	12	2	12	2	14	0	38	4
	Neutral	13	1	13	1	12	2	38	4
	Incompatible	13	1	12	2	13	1	38	4
Forced (left)	Compatible	13	1	13	1	12	2	38	4
	Neutral	12	2	12	2	14	0	38	4
	Incompatible	13	1	13	1	12	2	38	4
Forced (right)	Compatible	13	1	13	1	12	2	38	4
	Neutral	13	1	13	1	12	2	38	4
	Incompatible	12	2	13	1	13	1	38	4

N = trials with normal effects, D = trials with deviant effects.

Appendix C: Conditions for GLM Analysis in SPM

Table A2. Conditions in the general linear model (GLM) for fMRI analysis. Conditions 1-12 only contain trials with normal effects while conditions 13-19 were included in the model but not into further analyses. Separate models accounted for each of the three runs and excluded all error conditions without onsets in the respective run. All analyses were repeated with target-locked coding for condition 1-12 and replicated the results of the present model.

Condition	Choice	Comptaibility	Response	Onset
1	Free	Incompatible	Left	Response
2	Free	Incompatible	Right	Response
3	Free	Compatible	Left	Response
4	Free	Compatible	Right	Response
5	Free	Neutral	Left	Response
6	Free	Neutral	Right	Response
7	Forced	Incompatible	Left	Response
8	Forced	Incompatible	Right	Response
9	Forced	Compatible	Left	Response
10	Forced	Compatible	Right	Response
11	Forced	Neutral	Left	Response
12	Forced	Neutral	Right	Response
13	Incompatible	+ Deviant		Response
14	Compatible	+ Deviant		Response
15	Neutral	+ Deviant		Response
16	Deviant Effect			Effect
17	Error Type I			Response
18	Error Type II			Response
19	Error Type III			Target/Effect

Error Type I: anticipation or wrong keypress, ErrorType II: reaction to normal effect, double keystroke after deviant effect, or deviant reaction is carried out serially, Error Type III: miss (target-locked) or missed deviant effect (effect locked).

Appendix D: fMRI Contrast Free vs. Forced with Alternative Threshold

Table A3. Anatomical location, cluster size, MNI-coordinates, and peak statistics for the fMRI contrast Free vs. Forced, thresholded at $p < .001$, uncorrected, with a minimum cluster size of $k = 10$ contiguous voxels (see also **Table 1** for a more conservative evaluation). Only clusters with an overall $p_{FDR} < .050$ were considered.

Region	BA	Hemisphere	x	y	z	T	z	p_{FWE}	p_{FDR}
Prefrontal Cortex ($k_{left} = 1703$, $k_{right} = 3809$)								.000	.000
RCZ	6	L	-9	17	52	8.80	5.33	.003	.004
		R	0	20	46	8.41	5.22	.005	.009
SFG / SMA	6	L	-18	8	64	6.51	4.55	.099	.045
		R	18	11	64	10.88	5.87	.000	.004
MFG / DLPFC	9	L	-45	29	31	8.09	5.11	.009	.010
	46	R	45	35	34	10.01	5.66	.000	.004
PMC	6	L	-27	8	67	5.75	4.23	.273	.094
FEF		R	36	8	52	9.96	5.65	.000	.004
Orbitofrontal	11	L	-30	44	-8	9.15	5.43	.002	.006
		R	33	50	-14	5.30	4.02	.447	.151
Insula	13	L	-36	14	-2	8.31	5.18	.006	.009
		R	36	11	-2	8.28	5.18	.007	.009
Parietal Cortex ($k_{bilateral} = 2236$)								.000	.000
IPL	40	L	-42	-49	52	8.28	5.18	.007	.009
			-57	-49	49	7.86	5.04	.013	.501
		R	48	-43	46	9.18	5.44	.002	.006
SPL	7	L	-30	-61	52	6.77	4.65	.069	.035
		R	36	-61	52	6.68	4.62	.078	.038
Precuneus	7	L	-9	-76	46	6.46	4.53	.105	.048
		R	12	-73	49	5.76	4.23	.270	.094

continued overleaf

Region	BA	Hemisphere	x	y	z	T	z	p_{FWE}	p_{FDR}
Basal Ganglia (k_{left} = 51, k_{right} = 65) and Corpus Callosum (k = 189)								.000	.000
Pallidum	-	L	-15	-7	4	5.36	4.05	.441	.151
		R	15	-7	1	5.13	3.94	.558	.195
Corpus Callosum	-	-	0	-28	25	8.86	5.35	.003	.007
Occipital Cortex, Perioccipital Cortex, and Cerebellum (k_{left} = 817, k_{right} = 560)								.000	.000
Middle Occipital	19	L	-39	-73	4	7.4	4.88	.029	.019
Fusiform	37	L	-36	-55	-20	6.88	4.69	.060	.031
			27	-55	-17	5.76	4.23	.272	.094
Cerebellum	-	L	-45	-58	-35	4.95	3.84	.662	.242
		R	36	-55	-35	7.24	4.83	.036	.021

BA = Brodmann Area, RCZ = Rostral Cingulate Zone, SFG = Superior Frontal Gyrus, SMA = Supplementary Motor Area, MFG = Medial Frontal Gyrus, DLPFC = Dorsolateral Prefrontal Cortex, PMC = Premotor Cortex, FEF = Frontal Eye-Field, IPL = Inferior Parietal Lobule, SPL = Superior Parietal Lobule.

Appendix E: Interactive 3D-Model of the BOLD Response

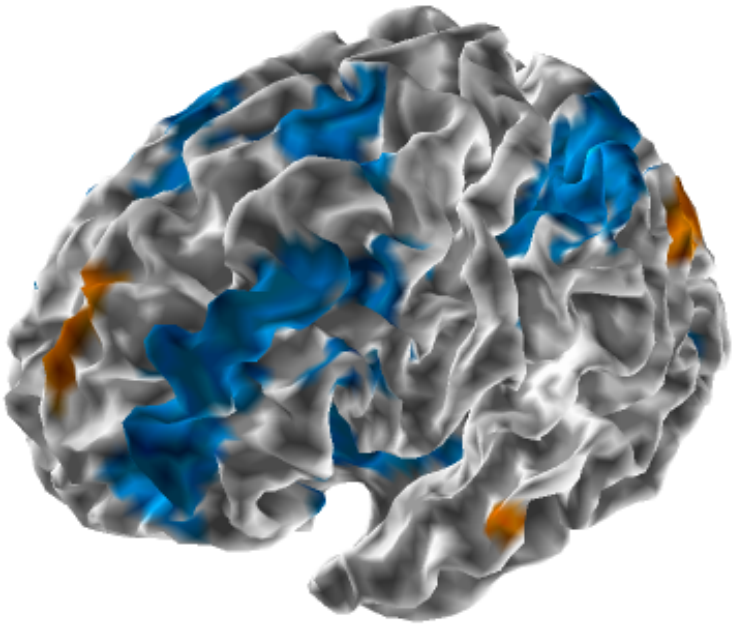

Figure A1. 3D-model of the contrast Free vs. Forced (blue) and Forced vs. Free (orange), thresholded at $p < .001$, uncorrected, and a minumum of $k = 10$ contiguously active voxels.

Appendix F: Are the Regression Results Caused by Black Magic?

Regression analyses with fMRI data have recently come into criticism as several publications used non-independent tests to produce correlation coefficients far beyond the limits of the reliability of both correlated measures ("vodoo correlations"; Vul, Harris, Winkielman, & Pashler, 2009; Vul & Kanwisher, in press; see Cureton, 1950 for a similar notion). And as the present experiment relies heavily on the correlation of R-E compatibility effects with the strength of the hemodynamic response, the possibility of artificially inflating this correlation has to be considered.

First of all, the reported correlations for the main contrast, Free vs. Forced, were obtained via single-step whole-brain analysis. Thus, no selection of active voxels took place which ensures independent data (Lieberman, Berkman, & Wager, 2009) and clear a priori hypotheses were formulated for all regions. The present results are further statistically warranted by the relatively high cluster threshold of k = 15 contigous voxels (Formann et al., 1995) and could also be replicated for both hand-secific contrasts (not reported here).

However, all correlations could still result from univariate and bivariate outliers (cf. Lieberman et al. 2009). To assess this possibility, I repeated the regression analysis for the most crucial region, BA 40, in two ways.

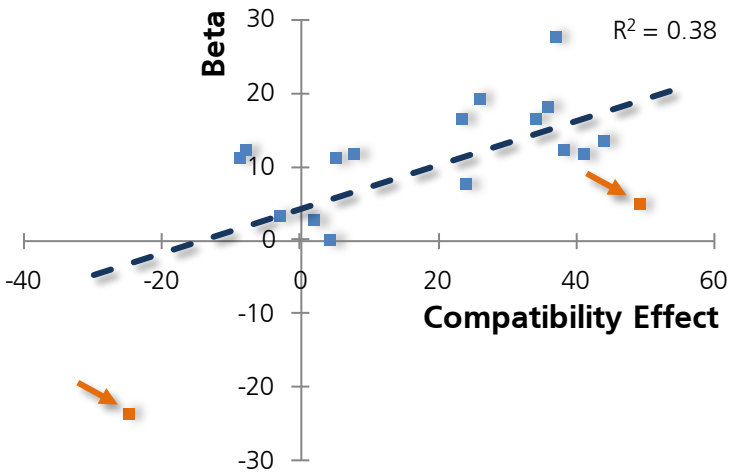

Figure A2. Correlation between signal strength (beta) and behavioural R-E compatiblity effect, computed across participants. The original correlation of r = 0.61, $t(16) = 3.09$, $p = 007$, was not affected when the two outliers were excluded from analysis, r = 0.57, $t(14) = 2.60$, $p = .021$. Accordingly, a direct comparison of both coefficients was not significant, $z = 0.17$, $p = .566$.

As a first assessment, I extracted the mean beta value of each participant for a sphere (10 mm radius) around the peak voxel of the regression analysis. Then, I z-standardised both, beta values and R-E compatibility effects for free choice trials of each participant to identifiy univariate outliers ($|z| > 1.96$) as well as bivariate outliers ($|z_{\beta}-z_{comp}| > 1.65$). One participant had to be excluded for each criterion and the following correlation of beta values and R-E compatiblity effects for the remaining participants produced comparable results (see **Figure A2**).

In order to assess the impact of outliers even more critically, I divided the participants into two groups: one group of the participants who showed a pronounced R-E compatibility effect and one group of the participants who did not show an R-E compatibility effect. The groups were created by a hierarchical cluster analysis on the individual R-E compatibility effects.[7] Then, the group factor served as new regressor in

[7] The cluster analysis used standard the Euclidean distance measure, between-groups linkage, and Ward's method for cluster fusion. A similar cluster analysis was performed on the individual *p*-values for *t*-tests for independent samples that compared RTs in compatible and incompatible free choice trials. This second cluster analysis produced the same grouping.

the fMRI contrast (again with a single-step, whole-brain analysis; cf. Lieberman et al., 2009) and reproduced the pattern of the original analysis (not shown here). Also, the mean beta values of the ROI around BA 40 proved to be different between both groups (14.83 vs. 3.58; $t(16) = 2.39$, $p = .029$, d = 1.14).

Thus, both re-assessments of the original correlation analysis produced highly convergent results. In combination with the methodological sound original analysis, these findings render the possibility of vodoo correlations highly unlikely.

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IMAGE REFERENCES

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Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig angefertigt und keine anderen, als die von mir genannten Quellen und Hilfsmittel, verwendet habe. [I declare that the research described in this thesis is my own work and that I only used the references and methods described in the text].

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