Neuroscience 231 (2013) 13–27

THE NEURAL SUBSTRATE OF THE IDEOMOTOR PRINCIPLE REVISITED: EVIDENCE FOR ASYMMETRIES IN ACTION-EFFECT LEARNING

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Abstract—Ideomotor theory holds that the perception or anticipatory imagination of action effects activates motor tendencies toward the action that is known to produce these effects, herein referred to as *ideomotor response activation* (IRA). IRA presupposes that the agent has previously learned which action produces which effects, and that this learning process has created *bidirectional* associations between the sensory effect codes and the motor codes producing the sensory effects. Here, we refer to this process as *ideomotor learning*. In the presented fMRI study, we adopted a standard two-phase ideomotor learning paradigm; a mixed between/within-subjects design allowed us to assess the neural substrate of both, IRA and ideomotor learning. We replicated earlier findings of a hand asymmetry in ideomotor processing with significantly stronger IRA by left-hand than right-hand action effects. Crucially, we traced this effect back to more pronounced associative learning for action-contingent effects of the left hand compared with effects of the right hand. In this context, our findings point to the caudate nucleus and the angular gyrus as central structures of the neural network underlying ideomotor learning.

Key words: motor control, executive functions, associative learning, caudate nucleus, fMRI.

INTRODUCTION

The term *ideo-motor* was coined in the middle of the 19th century, at a time when Europe was captivated by alleged paranormal phenomena ascribed to transcendent powers like table turning or magical pendulums (Tischner, 1929). Carpenter (1882) tried to explain these phenomena by referring to unwilled and unconscious motor excitation elicited by the anticipatory imagination (‘‘idea’’) of a specific effect. For instance, thinking of a swinging or rotating pendulum may unconsciously trigger tiny muscle activation in the fingers which hold the pendulum and thereby produce the imagined motion: the ‘‘*ideomotor reflex*’’.

Since then, the principle of triggering motor actions by effect anticipations has been embedded into a broad conceptual framework. Today, it is no longer seen as an involuntary reflex, bound to conditions of reduced will and expectant attention, but rather as a ubiquitous mechanism in voluntary action control – a truly executive function (James, 1890; see also Hommel et al., 2001; Pfister and Janczyk, 2012; Shin et al., 2010). In the following, we will refer to the mechanisms that relay sensory anticipations to motor centers as *ideomotor response activation* (IRA). This process relies on bidirectional associations between motor codes and sensory effect codes that have to be learned (Elsner and Hommel, 2001; Hoffmann et al., 2009). Once such action-effect associations have been acquired, activating a sensory effect code will automatically spread activation to the associated motor codes.

To put it in a broader theoretical framework, ideomotor assumptions can be related to general models of action control or limb praxis. One of the most influential theories of limb praxis was put forward by Rothi et al. (1991, 1997), a two-route model which distinguishes between the performances of familiar or meaningful movements on the one hand and unfamiliar or meaningless movements on the other. The former and only these would recruit on the so-called ‘‘output praxicon’’, a specialized long-term mnemonic structure which stores visuo-kinaesthetic attributes of movements, i.e. performance-related sensational or perceptual codes, which for movement execution are directly transcoded into motor programs. Entries of the output praxicon, in turn, get activated by more ‘‘passive’’ perceptual representations of physical characteristics (amplitude, spatial orientation, etc.) of actions, posited to be stored in another neurocognitive structure, the

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Abbreviations: BOLD, blood oxygen level dependent; FPC, frontopolar cortex; IRA, ideomotor response activation; SMA, supplementary motor area; TPJ, temporo-parietal junction.

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http://dx.doi.org/10.1016/j.neuroscience.2012.11.035

so-called ''input praxicon''. According to the theory, the input praxicon allows to identify familiar actions of the agent's repertoire, whereas the output praxicon supplies the motor implementation of actions at the innervatory pattern stage. Importantly, the outlined executive mechanism avoids the costs incurring for unfamiliar actions which require computing all the parameters needed to implement the spatial and temporal characteristics of intended movements (cf. Rothi and Heilman, 1996). There is an obvious similarity between the theoretically posited functionalities of output praxicon content on the one hand and learned action effects on the other, which are both assumed to be automatically transcoded into motor programs.

Similarly, ideomotor learning can be conceptualized as acquisition of a so-called *inverse internal model* (Wolpert and Kawato, 1998) which is a feedforward controller of motor action in which the output is identical to the input information. Basically, skillful coordinated limb movements arguably cannot be executed solely under feedback control, because feedback loops are generally slow and have small gains. Therefore, the brain needs to acquire an inverse dynamics model of intended action through motor learning, after which motor control can be executed in a pure feedforward manner (cf. Kawato, 1999; Wolpert and Ghahramani, 2000).

Whereas first neurophysiological studies have targeted the process of IRA (Elsner et al., 2002; Melcher et al., 2008; Kühn et al., 2011), the neural mechanisms underlying the preceding *ideomotor learning* are virtually unknown. Accordingly, the present study investigated the neural mechanisms underlying ideomotor learning and their relation to subsequent IRA.

To this end, we adopted a two-phase design that was previously used to assess the neurophysiological basis of IRAs (Melcher et al., 2008; cf. also Elsner and Hommel, 2001; Pfister et al., 2011). In an *acquisition phase*, participants performed key press actions to produce arbitrary action effects which in different subject groups were either contingent or non-contingent with the selected response. Thus, both groups had overall comparable sensory and motor activities but a different potential to exhibit ideomotor learning. In the subsequent *test phase*, participants of the contingency group were probed for IRA. Effect stimuli (i.e. stimuli which were presented as action effects during the acquisition phase) were now presented together with an imperative target stimulus[1], which prompted participants either to freely choose a response or to withhold responding (Fig. 1). No-go trials of the latter kind allow defining the neural correlates of the perception of learned action effects independent of proper motor activation: *the pure neural substrate of IRA* (cf. Elsner et al., 2002; Melcher et al., 2008). The presence of go trials on the other hand increases the response readiness of subjects and thus assumably promotes effects of IRA during no-go trials[2].

As outlined above, previous neurophysiological studies only investigated IRA (in more technical terms: the test phase) and neglected the underlying learning process (the acquisition phase). In these studies, IRA was mirrored in activity of the supplementary motor area (SMA) and the hippocampal system (Elsner et al., 2002; Melcher et al., 2008). The major goal of the present study was to investigate the learning process enabling such response activation effects. Interestingly, response activation effects in previous studies were entirely driven by structures associated with declarative memory such as the hippocampus or the parahippocampal gyrus. This medial temporal memory system is typically distinguished from a second, 'habit learning system' in the basal ganglia, i.e. comprising the putamen and caudate nucleus (e.g., Knowlton et al., 1996; Packard and Knowlton, 2002). Given that this second memory system was repeatedly associated with motor learning (see Seger, 2006, for a review), we expected ideomotor learning to draw on this system in addition to the medial temporal system (Tricomi et al., 2004).

Moreover, previous studies suggest that memory-based sensorimotor transformation or integration – i.e. output praxicon function (see above) – is represented in temporo-parietal regions. In this context, Peigneux et al. (2004), for instance, emphasized the contribution of the superior temporal cortex (superior temporal sulcus) in the sensory processing of action-related stimuli or proper motions. Rumiati et al. (2005) report a left-hemispherical pattern of increased activity comprising the inferior temporal gyrus and angular gyrus specifically in response to familiar actions, while Grèzes et al. (1999) related the inferior parietal cortex and the frontopolar cortex (FPC) to the acquisition of familiar actions during action observation (i.e. during visuomotor learning). Based on the outlined findings, ideomotor learning as a special instance of sensorimotor integration can be reasonably expected to rely on temporo-parietal regions in addition to genuine memory- or learning-related structures of the basal ganglia and the hippocampal system.

Furthermore, it is important to note that the described network for IRA found in previous studies only emerged for the left-hand but not for right-hand action-effects, indicating a fundamental asymmetry of ideomotor processes (cf. Melcher et al., 2008). Because the latter

[1] In the present work, we use the term ''target'' or ''target stimulus'' to denote task-relevant stimuli which one, according to the task-rules, has to recognize for response selection. These stimuli can be distinguished from non-targets, which have no direct relevance for task performance.

[2] In contrast to behavioral studies on ideomotor response activation (Dutzi and Hommel, 2009; Elsner and Hommel, 2001; Pfister et al., 2011; Hoffmann et al. 2009), the present study and the Melcher et al. (2008) study did not present effect stimuli as targets (i.e. task-relevant imperative stimuli) but only as additional stimuli accompanying the target. This procedure enables a within-subjects assessment of ideomotor response activations independent of proper motor activation by neurophysiological techniques (e.g. fMRI). This advantage, however, comes at the price of diminished behavioral effects. Accordingly, the present study did not find specific behavioral ''ideomotor'' effects for go trials at the regular statistical threshold – nor did Melcher et al. (2008) – which we expected and accepted already in the study planning. In the main manuscript we will thus focus exclusively on the neurophysiological data. A presentation of the behavioral data and related explications are given in Appendix.

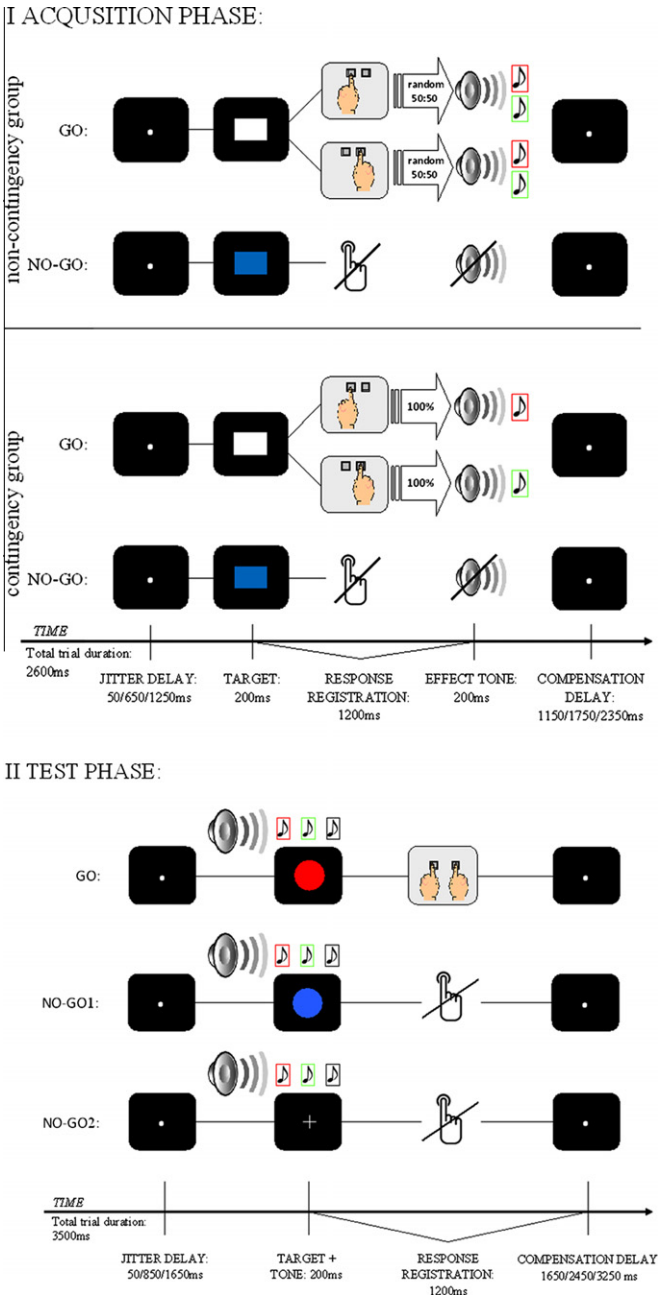

Fig. 1. Experimental set-up. The two-phase task set-up comprised of an acquisition phase (I) and a test phase (II), each of which involved a go/no-go task administered during fMRI. During the acquisition phase, subjects were presented with rectangles in either white or blue color serving as go and no-go signal, respectively. On go trials, subjects were to execute a free-choice response consisting of a button press with either the left or right index finger. Each button press on go trials produced an immediate auditory signal, a high- or low-pitched sinusoidal tone: the auditory action effect. The relation between response (i.e. button) location and tone pitch was varied in a between subject design with two experimental groups. In the *contingency group*, presses of one of the two buttons produced a high tone, while the opposite button produced a low pitch tone, with the side-tone mapping being counterbalanced across subjects (50% of the subjects received the low pitch tone for left responses and the high pitch tone for right responses, and inversely for the other 50%). In the *non-contingency group*, either button produced either tone in a random (unpredictable) order but about equally often across the whole task run. The acquisition phase served to identify the neural substrate of action-effect association learning (ideomotor learning) as evidenced by (between-subject) effects of contingency condition, separately for left-hand and right-hand action effects. In the following test phase, subjects of the contingency group performed another go/no-go task in which they carried out free-choice button press responses (of the same response set as in the acquisition phase). Simultaneously with the visual targets, tone signals were presented consisting either of one of the previous effect tones or a third medium pitch tone. Target stimuli were colored circles. Red circles served as go stimulus (go condition) and blue circles as no go stimulus (no-go1 condition). Additionally, we implemented trials in which a fixation cross instead of a colored circle was presented, which indicated no-go trials as well as blue circles. This latter trial type (no-go2 condition) was expected to include a relatively increased saliency of the tone signal and, thus, should yield an increased effect of tone type, i.e. of ideomotor condition. The test phase served to identify the neural substrate of ideomotor response activation as evidenced by (within-subject) effects of acquired response association of the tone signals presented during no-go trials. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

conclusion is based on ad hoc findings, it requires further empirical substantiation as well as theoretical elaboration and embedment. In this context, the Action-Perception model (Goodale and Milner, 1992; Milner and Goodale, 2010) emphasizes the differential skillfulness of left-hand and right-hand actions (which is based on the agent's handedness) as a factor which could mediate their differential proneness to ideomotor processes. The rationale behind is that motor actions which are not highly skilled are controlled by the ventral stream in the same way as perception, whereas highly skilled or automated actions are controlled by the dorsal stream. This functional neuroanatomical similarity of motor and sensory processes assumably facilitates sensorimotor integration including ideomotor processes (cf. Wiediger and Fournier, 2008). However, if motor codes of less skillful left-hand actions are indeed more easily bound to sensory codes of perceived stimuli, this should concern not only IRA but ideomotor learning too. Accordingly, in the present fMRI study, we basically aimed at (1) replicating results of asymmetric IRA in a slightly modified design and (2) to test for analogous asymmetries in the underlying ideomotor learning process. More specifically, based on the results of our previous investigation, we expected to observe increased IRA-related brain activations for the left-hand compared to right-hand learned action effects particularly in medial temporal structures as well as in premotor and supplementary motor cortices. An analogous left-/right-hand side asymmetry for ideomotor learning was expected to occur likewise in activations of medial temporal structures as well as in activations of the basal ganglia.

EXPERIMENTAL PROCEDURES

Participants

Thirty-six healthy, right-handed participants were recruited from the local university's student community. All subjects gave written-informed consent. They reported normal or corrected-to-normal vision, no history of psychiatric or neurological illness, and were currently not under psychotropic medication. Subjects were randomly assigned to one of the two experimental groups: 20 to the contingency group and 16 to the non-contingency group. Three subjects, however, had to be excluded from further analyses: one was unable to appropriately follow the task instruction, a second subject could not discriminate the presented tones, and a third subject exceeded the exclusion criteria of head movement greater than 3 mm and rotation greater than 3° during fMRI scanning. Of the remaining 33 subjects (18 females; mean age: 24.7 years), 18 were in the contingency group and 15 in the non-contingency group.

Design and procedure

Acquisition phase. In the acquisition phase, subjects performed a go/no-go task in which white rectangles signaled go trials and blue rectangles signaled no-go trials (Fig. 1, I). Go trials required a free-choice key press using either the left or right index finger. Subjects were instructed to react as spontaneously as possible but to choose both keys about equally often. Each key press produced an immediate auditory effect: either a 261-Hz sinusoidal tone (C0) or a 523-Hz sinusoidal tone (C1, i.e. one octave above C0). Tones were presented via headphones which simultaneously served as ear protection against the scanner noise.

We compared two experimental groups: for the *contingency group*, each key press contingently produced a tone of a particular pitch. Key-pitch mappings were counterbalanced across subjects to equate fMRI contrasts for sensory stimulation. For the *non-contingency group*, however, each key press produced one of the tones at random. Each acquisition trial started with the presentation of a white fixation cross presented for a variable time of 50, 650 or 1250 ms which served as event jitter to improve the MR data acquisition (oversampling) as well as the design efficiency (optimal event separation for statistical modeling). The fixation cross was followed by the target stimulus (appearing for 200 ms). Then, the screen was blanked until a total trial length of 2600 ms was reached. Responses were registered for 1200 ms after target onset and each response immediately triggered an effect tone (length: 200 ms). Error feedback was provided during no-go trials if subjects erroneously pressed one of the response buttons. In this case, subjects read "nicht drücken" ("Don't respond").

The event synchronization with the MR scanning – every second trial was triggered by an MR pulse – yielded a delay of about 200 ms after every second trial, which served as buffer to absorb temporal imprecision in the stimulation. The acquisition phase included a total of 160 go trials and 40 no-go trials.

Test phase. Only subjects of the contingency group proceeded to the test phase which was planned as a pure *within-subject* design in analogy to our previous study (Melcher et al., 2008). Nonetheless, subjects of the non-contingency group after the acquisition phase stayed in the scanner and performed a second task too, which however was administered to investigate another issue with no direct relation to the present study's purpose.

During the test phase, subjects responded to colored target circles that occurred simultaneously with a tone (Fig. 1, II). This tone was either one of the two previous action-effect tones (high- or low-pitch) or a third, medium-pitch tone (370 Hz; F#0)[3]. The visual target was red or blue. Red targets indicated go trials, in which subjects executed a free-choice response just as in the acquisition phase. As in the acquisition phase, blue targets signaled no-go trials, in which subjects were to withhold responding (the *no-go1* condition). Crucially, we included a second type of no-go trials during which a fixation cross instead of a blue circle was presented (the *nogo2* condition).

Thus, the no-go conditions differed with respect to the overall level of stimulation, with the nogo1 condition – closely resembling the situation in our previous study (Melcher et al., 2008) – including an overall increased stimulation as compared to the purer nogo2 condition in which the action effect stimuli should be able to gain relatively more attention and impact. From this, we expected to observe IRA effects not only for left-hand action effects, but for right-hand action effects too (even if to a lesser degree), while in the previous study IRA effects for right-hand action effects completely failed to appear.

Each test trial started with a fixation dot that appeared for a variable duration of either, 50, 850, or 1650 ms (serving as event jitter), followed by the visual target (colored circle or fixation cross; presented for 200 ms) and its accompanying tone. After target offset, the fixation dot was presented again until a total trial length of 3500 ms was reached. The synchronization of stimulation and scanning yielded a short

[3] We ran eight habituation trials between acquisition and test phase to avoid novelty effects of the medium-pitch tone. In these habituation trials, the new medium-pitch tone appeared in a consecutive sequence (tone length: 200 ms; ITI = 2200 ms) while subjects passively watched a fixation cross that simultaneously occurred with the tone.

delay of about 100 ms before the next trial began. The fMRI data analysis was restricted to no-go trials (nogo1 and nogo2), which allow for a direct assessment of IRA without neural noise effects of actual movements (cf. Melcher et al., 2008), whereas go trials ensured a high level of action readiness.

We ran 162 go trials, 162 nogo1 trials (visual target stimulus), and 108 nogo2 trials (fixation cross only) and each trial type featured an equal number of the three tones. A pre-defined trial sequence ensured that each trial type followed each other trial type equally often. We included a reduced number of nogo2 to keep the experiment as compact as possible. We expected the nogo2 condition to absorb this slight reduction in statistical power due to the expected increased ''power'' of IRA when no competing visual information is presented. Depending on the presented tone signal, three types of no-go trials could be distinguished for the analysis of both, the nogo1 and the nogo2 condition: (1) *no-go left* if the presented tone was associated with a left-hand response, (2) *no-go right* if the presented tone was associated with a right-hand response, and (3) *no-go neutral* if the medium-pitch tone (i.e. the tone without response association) was presented.

fMRI data acquisition and pre-processing

Imaging was performed with a 3 T MRI scanner (Magnetom TIM Trio, Siemens Healthcare, Erlangen, Germany) equipped with a standard eight channel phased-array head coil. Prior to functional scanning, we acquired a T1-weighted anatomical dataset at 1-mm isotropic resolution. Functional scans consisted of 29 axial slices covering the entire brain (parallel to the AC-PC plane). Slices were obtained in ascending order (thickness = 3 mm; distance factor = 5%) using a gradient-echo echo-planar imaging (EPI) sequence (echo time = 30 ms; flip angle = 70°; field-of-view = 192 mm). Imaging was separated in four sessions of 300, 315, 299, and 299 volumes (total: 1213 volumes) with an inter-scan repetition time (TR) of 1800 ms. The first session was the acquisition phase and sessions 2–4 constituted the test phase; session 2 included initial habituation trials (cf. footnote 2). Using the SPM5 software package (http://www.fil.ion.ucl.ac.uk/spm/), the functional images acquired were realigned, corrected for motion artifacts (SPM5 procedure 'Realign & Unwarp'), global signal intensity variation, and low-frequency fluctuations (high-pass filter with 128-s cutoff), normalized into standard stereotactic space (MNI template), and spatially smoothed with a 9-mm full-width at half-maximum Gaussian kernel. For statistical analysis of the functional images, the experimental conditions were modeled by the convolution with a hemodynamic response function accounting for the delay of the BOLD (blood oxygen level dependent) response. Event onset was locked to the auditory stimulus for both, acquisition and test trials. The analysis was based on a least-squares estimation using the general linear model for time-series data on a voxel-by-voxel basis. The statistical models (random effect ANOVA models) applied to determine the effects of interest are explicated in the following two sub-sections.

fMRI data analysis I: acquisition phase

To investigate brain activation related to ideomotor learning, we modeled parametric modulations of condition-specific brain activation by time. Basically, BOLD responses have been modeled to the presentation of the auditory stimulus (i.e. the action effect), using event-related temporal basis functions to create separate regressors for left-hand and right-hand action effects. Additionally, the created condition regressors were multiplied with a linearly increasing function leading to a linear time-by-condition interaction, i.e. a first-order time modulation (cf. Büchel et al., 1998; Toni et al., 2001; Eippert et al., 2008). Time-modulated regressors can mirror time-dependent changes (either increases or decreases) of brain activity in the different experimental conditions, which are independent of the condition's main effects. In the single-subject analysis, the time-modulated conditions have been contrasted against implicit baseline (i.e. were set to 1 with the other condition set to 0) to create one beta image for each condition. For the group analysis, the single-subject beta images of the learning regressors (i.e. the time-modulated condition regressors) were entered into a random-effects 2×2 ANOVA model with contingency (between-subjects: contingent vs. non-contingent) and response side (within-subjects: left-hand vs. right-hand) as factors, resulting in the following four cells (i.e. conditions): (A) left response/contingency group (B) right response/contingency group (C) left response/non-contingency group (D) right response/non-contingency group. Within this ANOVA model, we computed condition contrasts to define main effects and interaction effects of the included factors. More specifically, we contrasted the groups against each other (contingent vs. non-contingent) to define learning effects for left-hand and right-hand action effects (contrasts: A–C and B–D). These contrasts should reveal activation drifts (increases or decreases), which are significantly stronger for the processing of contingent action effects compared to otherwise identical non-contingent action effects. *As groups only differ in this factor (i.e. the contingency of action effects), defined between-group differences can be unequivocally interpreted as neural substrate of association learning*. Moreover, learning effects for left-hand and right-hand action effects have been contrasted against each other to define learning-related brain activations (activation increases or decreases) which are different for the two response sides (contrasts: (A–C)–(B–D) and (B–D)–(A–C)). This is the interaction between the two ANOVA factors. All findings of the random-effects analysis were thresholded at $p < .001$, uncorrected, with a minimum cluster size of 10 contiguous voxels.

In order to ensure a straightforward interpretation of findings of the acquisition phase, we applied a masking procedure to the group comparisons (between-subjects contrasts). More specifically, we used the learning regressors of the contingency group as inclusive mask (tested against implicit baseline at $p < .100$), which was set to either 1 or -1 reflecting activation increases and decreases in this group, respectively. Then, group comparisons to reveal stronger activation increases for the contingency compared to the non-contingency group (contrast: ''contingent minus non-contingent'') used the respective mask set to 1, whereas group comparisons to reveal stronger activation decreases for the contingency group (contrast: ''non-contingent minus contingent'') used the respective mask set to -1. *This masking ensured that findings of relative stronger activation decreases in the contingency group indeed reflect proper activation decreases rather than factual activation increases which are relatively reduced in the contingency compared to the non-contingency group (and vice versa for activation increases)*. Since no small volume correction was applied, the masking did not affect the statistical threshold, i.e. did not cause an increase of alpha error probability.

fMRI data analysis II: test phase

BOLD responses in the test phase have been modeled to the presentation of the tone stimulus (event-related modeling), which appeared simultaneously with the visual target stimulus. This model included the following basic experimental conditions: *(A) no-go left* (no-go trials in which the tone associated with a left response was presented), *(B) no-go right* (no-go trials in which the tone associated with a right response was presented), and *(C) no-go neutral* (no-go trials in which the medium pitch tone which did not appear during the acquisition phase was presented). In the single-subject analysis, conditions have been contrasted against implicit baseline (set to 1 with the

other conditions set to 0) to create one beta image for each condition. For the group analysis, single-subject beta images of the three no-go trial types were subjected to a one-way repeated-measures ANOVA (random effects model). We created two separate ANOVA models for nogo1 and the nogo2 conditions. Within the ANOVA models, we conducted pairwise comparisons between the three no-go trial types in order to define brain activations related to IRA by left-hand and right-hand learned action effects separately (contrasts: A–C and B–C) as well as to directly compare IRA effects for the two response sides (contrasts: A–B, and B–A). All findings were thresholded at $p < .001$, uncorrected, with a minimum cluster size of 30 contiguous voxels.[4]

Furthermore, we conducted correlation analyses to relate the findings of acquisition and test phase by means of a regression model which we applied to the fMRI data. These additional analyses were motivated by the fact that stronger activation increases or decreases for contingent compared to non-contingent action effects do not necessarily reflect proper ideomotor learning (bidirectional association between action and action effect) but may reflect a simpler associative learning process leading to merely unidirectional action-effect associations. Such unilateral associations would only allow to anticipate sensory effects (i.e. activate sensory effect codes) when performing an action but not to activate motor codes from the mental representation of action effects. To identify those brain regions that are specifically involved in ideomotor learning, we tried to statistically relate learning-related brain activations during the acquisition phase to neural measures of IRA during the later test phase. In this context, we considered increased hippocampal activation in relation to the perception of learned action effects as the most direct and unequivocal neural indication of IRA which – in its core – represents a memory retrieval process consisting in the recall of the learned association between action and action effect. Moreover, the hippocampus is the region which has been most consistently related to IRA in previous studies (cf. Melcher et al., 2008; Elsner et al., 2002). *Hence, the basic question of the described regression analyses was whether brain activations related to learning during the acquisition phase indeed predict memory retrieval during the later test phase.*

Technically, we created regression models (SPM random-effects model ''multiple regression'') which specifically tested which of those regions that exhibited significant learning-related activation during the acquisition phase reliably predicted hippocampal activation in the later test phase. More specifically, we extracted single-subject beta values for ROIs defined as spheres ($r = 10$ mm) around the peak coordinates of the learning-related activations using the respective learning regressor for left-hand or right-hand action effects. Both, ROI definition and beta extraction used the MarsBaR toolbox (http://marsbar.sourceforge.net/). The dependent (i.e. predicted) variable of the regression was the hippocampal activation related to IRA during the test phase which we defined by the contrasts ''action effect vs. neutral tone'' (for left-hand and right-hand action effects, separately) spatially restricted to the bilateral hippocampus. For this purpose, we used the AAL brain atlas (running on SPM5) to create a region of interest (i.e. a masque) which comprised the whole left and right hippocampus. In order to accommodate the spatial restriction of the analysis, the statistical threshold for the regression analysis was set to $p < .05$ (FWE-corrected for multiple tests; small-volume correction). Considering the spatial restrictions of the hippocampus, we applied a reduced extent threshold of five contiguous voxels.

[4] In the presented fMRI data analyses, we did not rigorously control for multiple testing (family-wise error rate), but instead applied uncorrected p values together with a spatial extent threshold to control for false positive rates (cf. Forman et al., 1995). In this context, we want to emphasize that the present study was designed to test specific and well-grounded hypotheses and thereby (in part) to replicate previous results in a different context.

RESULTS

Acquisition phase: neural substrate of action-effect association

Contrasts of the learning regressors are listed in Table 1 and particularly for left-hand action effects visualized in Fig. 2. In a nutshell, we found stronger activation decreases for contingent than for non-contingent action effects for both hands, but we did not observe any stronger activation increases. Contingent right-hand action effects showed a stronger decrease of brain activation in the rostral (perigenual) anterior cingulate cortex, reaching into the corpus callosum ($t = 4.51$; MNI-coordinates: 3 30 12; $k = 23$ at $p < .001$). In contrast, contingent left-hand action effects exhibited a widespread pattern of significant activation decreases comprising of the caudate nucleus, the FPC, the angular gyrus, superior frontal gyrus, inferior temporal gyrus, as well as the posterior hippocampus and adjacent parahippocampal gyrus.

A direct comparison of contingent left-hand and right-hand action effects confirmed significantly stronger activation decreases for left-hand action effects in two regions: the hippocampus and the superior temporal sulcus. Contingent right-hand compared to contingent left-hand action effects, on the other hand, exhibited no significantly stronger activation decrease.

Test phase: neural substrate of IRA

At the statistical threshold used, contrasts of the nogo1 condition (blue circle accompanied by a tone) revealed no differential activations between action effects and the neutral tone, which was true for left-hand and right-hand action effects. In other words, there was no indication of IRA in the nogo1 condition. However, nogo2 trials (tone without competing visual stimulation) did exhibit substantial effects of IRA (Table 2), which replicates and extends the findings from our previous study (Melcher et al., 2008; for a direct comparison between findings of the two studies, see Appendix). First, there was significantly increased activation for left-hand action effects (compared to neutral tones) in a network comprising bilateral premotor cortex, right primary motor cortex, motor-related regions in the frontomedian wall (pre-SMA, RCZ), caudate nucleus, inferior frontal gyrus, insula, FPC, (posterior) intraparietal cortex, precuneus, temporo-parietal junction (TPJ), and the hippocampus as well as parahippocampal cortex.

At the same time, the analogous contrast for right-hand action effects exhibited a substantially weaker effect. Still, however, this effect was stronger than in the Melcher et al. (2008) study where no differential activations between right-hand action effects and neutral tones were observed. Brain regions showing significantly increased activation for right-hand action effects comprised of motor-related regions in the medial frontal wall, insular cortex, and the posterior cingulate gyrus. Importantly,

Table 1. Results of the acquisition phase. Significant findings of condition contrasts computed within a 2 × 2 mixed ANOVA model including two factors: (a) group (contingency vs. non-contingency) and (b) response side (right-hand vs. left-hand action effect). Findings were thresholded at $p < .001$ ($k \geqslant 10$). This threshold was lowered stepwise (to $p < .005$ and $p < .01$) in order to complete the descriptive comparison of left-hand and right-hand action effects. Findings defined at a lowered threshold are listed in brackets in order to emphasize that these do not reflect main findings but should only provide a further explanation of findings defined at the conservative threshold

Region	Left-hand action effects (contingent > non-contingent)			Right-hand action effects (contingent > non-contingent)			Left-hand > right-hand (interaction contrast)			Right-hand > left-hand (interaction contrast)		
	MNI coordinates	*t* value	*k*	MNI coordinates	*t* value	*k*	MNI coordinates	*t* value	*k*	MNI coordinates	*t* value	*k*
L posterior hippocampus/ parahippocampal gyrus	−24 −30 −12	4.51	26	n.s.			−24 −30 −15	3.96	17	n.s.		
L middle temporal gyrus/inferior temporal sulcus	−51 −18 −18	4.51	12	n.s.			[−48 −15 −21]	3.66	[10*]	n.s.		
L anterior superior frontal gyrus	−15 45 33	4.34	63	n.s.			[−18 45 33]	2.60	[9**]	n.s.		
R head of caudate nucleus	3 15 −3	3.72	11	[0 15 0]	3.63	[21*]	n.s.			n.s.		
L angular gyrus	−42 −66 27	3.64	27	[−45 −66 30]	3.10	[5*]	n.s.			n.s.		
R anterior medial frontal wall/frontopolar cortex	9 60 12	3.49	10	[9 63 9]	2.53	[3**]	n.s.			n.s.		
L superior temporal sulcus	[−51 −30 0]	2.90	[48**]	n.s.			−54 −24 −3	3.76	48	n.s.		
R anterior cingulate/ corpus callosum	n.s.			3 33 12	4.24	20	n.s.			[3 27 15]	2.89	[4*]

$p < .001$; $k \geqslant 10$.
n.s.: not significant/no suprathreshold activation.
* Lowered threshold: $p < .005$ (no clusterthreshold).
** Lowered threshold: $p < .01$ (no clusterthreshold).

activations for right-hand action-effects broadly overlapped with the activations for left-hand action effects. Other regions activated by left-hand action effects were significant for right-hand action effects only at a lowered statistical threshold and included bilateral premotor cortex, TPJ, and the hippocampus.

A direct comparison between left-hand and right-hand action effects revealed a number of brain regions showing significantly increased activation for left-hand action effects (see Fig. 3), but no brain regions with stronger activation for right-hand compared to left-hand action effects, thus confirming the prediction of a basic asymmetry of IRA.

Correlation analyses: bridging ideomotor learning and IRA

As pointed out above, stronger activation decreases for contingent compared to non-contingent action effects do not necessarily reflect bidirectional ideomotor learning but may reflect a simpler associative learning process leading to unidirectional action-effect associations. To define those brain regions that are specifically involved in bidirectional ideomotor learning, we correlated the learning-related activation decreases in the contingency group with an index of IRA – more precisely with the increased hippocampal activation in response to learned action effects as compared with otherwise equivalent non-effect tones.

Two out of the six learning-related activations were significantly correlated with hippocampal activation in response to left-hand action effects during the test phase: the caudate nucleus and the angular gyrus. More specifically, learning-related activation in the caudate nucleus predicted IRA-related activation in the left hippocampus (peak coordinates: −27 −24 −9; $t = 6.77$; $k = 10$) and also in the right hippocampus (peak coordinates: 24 –33 0; $t = 7.77$; $k = 7$). The activation decreases in the angular gyrus exhibited a significant relation exclusively to the right hippocampus (two foci; peak coordinates: 30 –24 −9/15 –9 −15; $t = 7.39/6.39$; $k = 6/7$).

Following the results for left-hand action effects, we built an additional regression model for right-hand action effects to look for analogous relations between activation decreases during the acquisition phase and later effects of IRA. In addition to the caudate nucleus and the angular gyrus, we included the region in the ACC which had exhibited significant learning-related activation specifically for right-hand but not for left-hand action effects. Basically, none of the three regressors exhibited a significant relation to hippocampal activation in the test phase, clearly demonstrating a fundamental hand-asymmetry in ideomotor learning.

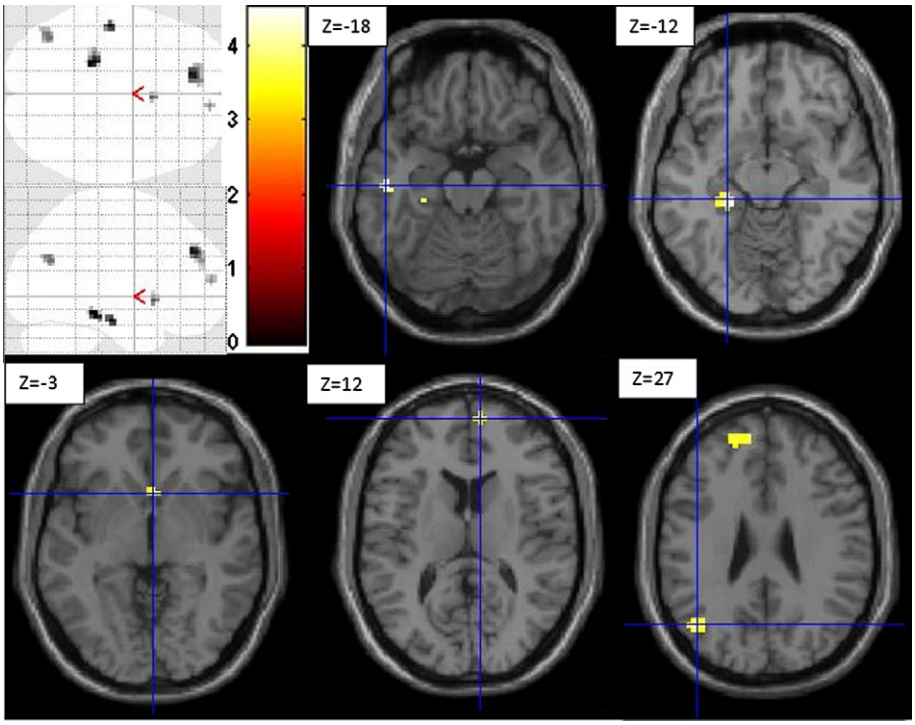

Fig. 2. Results of the acquisition phase. Brain regions exhibiting a significant learning effect for left-hand action effects, in terms of a significant decrease of activation for contingent as compared to non-contingent left-hand action effects. Activations are superimposed onto horizontal slices of the MNI template (neurological orientation). Activations were localized in the inferior temporal sulcus, the hippocampus, nucleus caudatus, frontopolar cortex, and angular gyrus (in the order of the slices from top left to bottom right). Activations were determined in a random effects between-subject analysis thresholded at $p < .001$ and $k \geqslant 10$.

DISCUSSION

The present study investigated neural mechanisms that underlie ideomotor processing, particularly the acquisition of action-effect associations by *ideomotor learning* and the later activation of motor tendencies by the learned action effects (cf. Elsner et al., 2002; Melcher et al., 2008; Kühn et al., 2011).

To our knowledge, this is the first study to investigate the neural substrate of bidirectional action-effect learning. For this purpose, we used a time-by-condition interaction analysis that compares time-modulated brain activity (i.e. linear activation courses – increases or decreases) across the processing of a sequence of contingent vs. non-contingent action effects. Several structures were found to mediate ideomotor learning, such as hippocampus, parahippocampal gyrus, caudate nucleus, and angular gyrus. Crucially, these activations comprised areas that are traditionally ascribed to two distinct systems subserving learning and memory. The medial temporal (hippocampal) memory system is typically related to declarative memory whereas the basal ganglia (e.g., the caudate nucleus) are related to motor control and operant conditioning (Knowlton et al., 1996; Packard and Knowlton, 2002; Seger, 2006; Yin and Knowlton, 2006). These findings extend previous reports on IRA that only found evidence for the involvement of medial temporal memory systems in ideomotor action control (Elsner et al., 2002; Melcher et al., 2008).

The exact relation of both memory systems has been debated over the last decades (e.g., Packard and Knowlton, 2002; Myers et al., 2003). Thus, some studies found evidence for independent processing (Reber and Squire, 1998) whereas other settings gave rise to direct competition between both systems (Poldrack et al., 2001). This research suggests that the type of task and learning process might determine whether both systems interact or operate independently and – in case of an interaction – whether they compete or work in concert. Our study shows that both systems are relevant for the acquisition of bidirectional response-effect associations and interact during the learning process. Furthermore, learning-related activity in the caudate nucleus predicted later IRA as mirrored in hippocampal activity, indicating that both systems contribute to (rather than compete for) ideomotor learning.

But what is the function of the basal ganglia for ideomotor learning? Converging evidence from both, human and animal studies relates the anterior caudate nucleus to conditional motor learning, i.e. the incremental acquisition of stimulus–response associations (e.g., Packard and Knowlton, 2002; White and McDonald, 2002; Voermans et al., 2004). In this context, the function of the nucleus caudatus has been described as consisting in the weightening of associations between exteroceptive stimuli and motor actions (Williams and Eskandar, 2006). The present study suggests a very similar sensorimotor associative function of the caudate nucleus in the processing of exteroceptive action effects and, hence, a key role in ideomotor learning.

Table 2. Results of the test phase. Significant findings of condition contrasts computed within a one-way ANOVA model including the following three conditions: (a) left-hand action effect, (b) right-hand action effect, and (C) neutral (non-effect) stimulus. Findings were thresholded at $p < .001$ ($k \geqslant 30$). This threshold was partly lowered (to $p < .005$; $k \geqslant 10$) in order to supplement the descriptive comparison between left-hand and right-hand action effects in the table. Findings defined at the lowered threshold are listed in brackets in order to emphasize that these do not reflect main findings but should only provide a further explication of findings defined at the conservative threshold

Region	Lleft vs. neutral			Right vs. neutral			Left vs. right			Right vs. left	
	Coordinates/ statistical effect (*t*-value)		*k*	Coordinates/ statistical effect (*t*-value)		*k*	Coordinates/ statistical effect (*t*-value)		*k*	Coordinates/statistical effect (*t*-value)	*k*
L/R pre-SMA/RCZ/ anterior cingulate	3 36 45	5.61		6 39 45	4.53						
	3 21 45	4.73		0 27 45	4.04	396	n.s.				
	−9 39 18	4.41		−9 33 12	4.48						
L frontal operculum/ anterior insula	−54 12 15	4.63		n.s.			−60 3 12	4.13	77		
	−42 12 0	3.87	932				n.s.				
	−24 24 −12	3.86		−24 24 −6	4.24	31					
L inferior premotor cortex	−51 −3 15	3.28		n.s.			−51 −3 18	4.24			
L/R caudate (head)	−6 12 6	4.42		[−6 12 9]	3.50	[73*]	n.s.				
	6 12 6	3.99		n.s.			[6 15 6]	2.98	[5*]		
L inferior frontal gyrus/ pars triangularis	−42 42 6	4.07	63	[−51 30 12]	3.55	[94*]	n.s.				
R dorsal premotor cortex (FEF)/SFG	27 9 57	4.39	146	[27 18 45]	3.53	[1335*]	33 −9 51	4.20	49		
L premotor cortex/motor cortex	−39 3 51	4.46	368	[−39 6 51]	3.05	[35*]	[−30 −9 54]	3.17	[51*]		
	−45 12 39	4.14		[−42 9 45]	3.09		n.s.			No suprathreshold activation	
R primary motor cotex/ central sulcus	30 −30 51	3.93	43	n.s.			[24 −36 54]	3.15	[20*]		
R FPC/mOFC	6 54 −6	4.33	54	9 51 −12	4.25	80	n.s.				
L/R posterior cingulate cortex	−6 −18 39	5.10	120	[−6 −21 36]	3.31	[11*]	n.s.				
	15 −9 39	3.52	62	n.s.			[−3 6 39]	3.79	[118*]		
L/R paracentral lobule	−9 −30 60	4.62		n.s.			−6 −27 60	3.61	36		
	6 −33 63	3.52		n.s.			9 −33 63	3.74			
L intraparietal cortex/ anterior IPS	−27 −60 57	4.37	240	n.s.			−24 −63 54	4.61	213		
	−21 −81 42	3.73					−21 −78 42	4.09			
L/R TPJ	−45 −45 21	4.35	69	n.s.			[−63 −45 27]	3.72	[61*]		
	39 −48 15	3.98	175	[36 −51 15]	3.11	[11*]	[48 −54 0]	3.33	[23*]		
L/R superior occipital cortex	30 −72 18	3.99		[27 −75 6]	2.85	[70*]	n.s.				
	−36 −90 24	3.96	30	n.s.			[−24 −84 21]	3.99	[213*]		
R precuneus	12 −54 63	4.10	90	[12 −54 63]	3.16	[5*]	n.s.				
L hippocampus	−33 −15 −15	4.17	31	[−24 −30 −15]	3.93	[203*]	n.s.				
R parahippocampal gyrus	[42 0 −9]	3.66	[45*]	n.s.			45 −3 −15	5.26	55		
L caudate (tale)	−12 −9 18	3.86	30	[−21 −12 21]	2.87	[33*]	n.s.				

Prior studies related the nucleus caudatus to behavioral goal achievement, i.e. to the processing of feedback information which signals appropriate or successful performance independent of whether this is related to an external reward (e.g., Tricomi and Fiez, 2008; Lutz et al., 2012). The detection of contingencies in the outcome of one's actions may be likewise considered a kind of goal-achievement which highlights

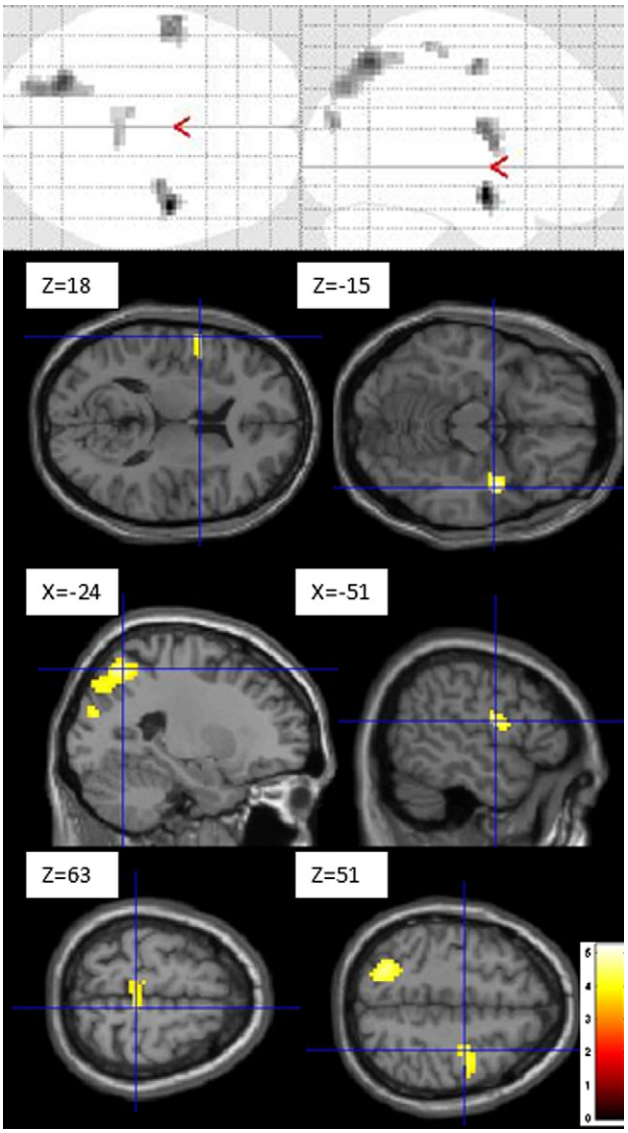

Fig. 3. Results of the test phase. Brain regions exhibiting significantly increased activation (i.e. an increased IRA-effect) for left-hand compared to right-hand learned action effects, superimposed onto horizontal and sagittal slices of the MNI template. Activations were localized in the insular cortex, parahippocampal cortex, intraparietal cortex, ventral premotor cortex, paracentral lobule, as well as the dorsal premotor cortex (in the order of the depicted slices from top left to bottom right). Activations were determined in a random effects analysis thresholded at $p < .001$ and $k \geqslant 30$.

an additional functional facet of ideomotor learning. More specifically, the experience of contingent action effects can be assumed to strengthen the sense of self-determination and thus to be intrinsically rewarding (cf. Sansone and Smith, 2000). Accordingly, agents assumably not only passively notice contingencies in their action consequences but rather actively search for them. Such a mechanism of active contingency monitoring can be considered highly adaptive because knowledge about action consequences is a – or even the – mainstay of behavioral control and effectiveness.

A second region highlighted as neural substrate of ideomotor learning in the present work was the angular gyrus, which has been conclusively related to motor learning – and particularly to its sensory aspects – in other contexts, too (cf. Grèzes et al., 1999; Rosenthal et al., 2009). Moreover, this regions has been implicated in the guidance of motor actions by internal sensory representations (e.g., Kawashima et al., 1995), in the processing or monitoring of action consequences (Farrer et al., 2003), as well as in the experience of agency (Farrer and Frith, 2002). The basic neurocognitive function of the angular gyrus underlying the mentioned processes can be conceptualized as ‘‘computation of action awareness representations’’ (cf. Farrer et al., 2008). In other words, the angular gyrus may be considered to provide conscious access to different sensory aspects of one’s own actions which are closely related to intention. This neurocognitive function also provides a highly plausible description of the angular gyrus’ involvement in ideomotor learning. Other brain activations of the acquisition phase appeared to be related more basically to association learning and, thus, may be considered to contribute only indirectly to ideomotor learning. These activations occurred likewise specifically for left-hand action effects and mainly comprised the left middle and superior temporal cortex as well as the right FPC. The found temporal activation foci are located inferior to the primary auditory cortex and can be ascribed to the auditory association areas (Brodmann’s areas 21 and 22) which interpret and integrate auditory sensations. Activations in the middle and superior temporal cortex in the left hemisphere have been previously described as an important neural substrate of the ‘‘output praxicon’’ storing visuokenetic features of familiar actions which guide action execution (Peigneux et al., 2004; Rumiati et al., 2005, 2010; see Introduction). Accordingly, temporal activations in the present work may be considered to represent the specific (high- or low-pitch) effect stimuli as auditory features of the respective button press responses to enable the acquisition of sensorimotor associations as genuine memory function.

Important to note, all defined learning-related activations were stronger activation decreases in the contingency group (compared to the non-contingency group), while no differential activation increases between groups were observed. Generally, functional activation decreases related to learning are a quite common finding both in human and animal studies, and have been particularly observed in the basal ganglia and the hippocampal system (e.g., Carelli et al., 1997; Grafton et al., 2002; Delgado et al., 2005). In this context, it has been suggested that activation decreases reflect that respective regions are involved particularly in the early stages of learning with an evolving adaptation following afterward when acquired associations or memory traces consolidate (cf. Poldrack et al., 1999; Packard and Knowlton, 2002).

Importantly, learning-related brain activations in the present study were consistently reduced for right-hand compared to left-hand action effects. Furthermore, learning-related asymmetries were mirrored in IRA effects that replicated prior findings (cf. Melcher et al.,

2008). Taken together, these results suggest a fundamental asymmetry of ideomotor processes being significantly more involved in left-hand compared to right-hand actions. This conclusion is well in line with the assumption that left-hand and right-hand actions, based on their differential skillfulness, rely – at least in part – on different neural control mechanisms. More specifically, according to the Action-Perception model (Goodale and Milner, 1992; Milner and Goodale, 2010), all actions that are not highly skilled are controlled by the ventral stream in the same way as perception, whereas more skilled and automatic actions are controlled by the dorsal stream. This functional distinction directly leads to the notion that unskilled actions rely more on sensory information, which of course should include sensory representations of learned action effects, which are provided by the ventral pathway (cf. Wiediger and Fournier, 2008).

The present study, however, also found several regions to be equally involved in IRA of the left and the right hand, suggesting that functional differences between left-hand and right-hand actions are more quantitative than qualitative in nature. Most prominently, there was significantly increased activation for both, left-hand and right-hand action effects in regions of the frontomedial wall (comprising the anterior cingulate, pre-SMA and more anterior medial SFG). These regions are considered to be central instances of the neural motor system (e.g., Fink et al., 1997). Moreover, these regions have been repeatedly related to the triggering of motor tendencies by exteroceptive sensory stimuli in general and learned action effects in particular (e.g., Elsner et al., 2002; Gazzola et al., 2006; Mutschler et al., 2007; Melcher et al., 2008). Further activations shared by left-hand and right-hand action effects were observed in the FPC as well as in the left anterior insular and adjacent frontal operculum, presumably overlapping with the insular sensorimotor hand representation (cf. Burton et al., 1993; Fink et al., 1997). In one related study, this latter region was specifically activated when subjects listened to musical sequences which they before actively played on the piano compared to otherwise equivalent melodies which they only knew from listening (Mutschler et al., 2007). Together with the present work, this suggests a basic ''*mirror property*'' of the anterior insular cortex yielding (re-)activations of motor representations by associated exteroceptive stimuli.

In addition to the reported hand asymmetry, our findings point toward a second boundary condition for IRA concerning the saliency of stimuli and action effects for ideomotor processing. Interestingly, pronounced effects for IRA only emerged when previous action effects were presented without competing visual information. In contrast, IRA was absent when we introduced competing task-related visual stimulation. This has the theoretical implication that IRA is not a truly automatic process but, minimally, requires the availability of sensory- or attentional-processing resources. This conclusion is in line with behavioral studies on the role of task-relevance and salience for other ideomotor tasks (e.g., Ansorge, 2002; Hommel, 1993; see also Pfister et al., 2010a,b). Supporting the present conclusion, these studies suggested that the anticipation of distal action effects is also moderated by different factors such as instructions specifying action effects as task-relevant.

The theoretical notion that hand asymmetries in ideomotor processes may rely on differential skillfulness as described in the Action-Perception model raises interesting issues for future studies. First, future studies may investigate whether asymmetries in ideomotor processes still persist when the critical contingent feature of the action effect is presented in another stimulus dimension (e.g., sound instead of pitch) or a different stimulus domain (i.e. when presenting visual or tactile effect stimuli instead of tones). Thereby, one can also accommodate the objection that hand asymmetries may be bound to the specific effect stimuli used in the present task paradigm and, accordingly, may be not a genuine property of ideomotor processing. Second, it is an issue of high relevance whether left-handed subjects exhibit an asymmetry inverse to the one in right-handers. This finding would support skillfulness as crucial factor in ideomotor processing whereas an accordant asymmetry in left-handed subjects would require a different theoretical account.

CONCLUSIONS

In the present work, we investigated the neural mechanisms underlying ideomotor processing, i.e. the acquisition of action-effect associations (ideomotor learning) and the triggering of motor activation by the perception of learned action effects (IRA). We were able to replicate earlier findings of a hand asymmetry in IRA (significantly stronger for left-hand compared to right-hand learned action effects) which we traced back to an analogous hand asymmetry in ideomotor learning. Crucially, to our knowledge, this is the first study to investigate the neural substrate of ideomotor learning. Our results indicate the caudate nucleus and angular gyrus as key regions in this process which represents a special instance of associative (sensorimotor) learning. These results extend previous findings on the role of medial temporal memory systems for ideomotor action control and point toward an interaction of these systems with learning-related regions within the basal ganglia.

Acknowledgments—We thank Mr. Timo M.D. Graen (M. Sc. in Physics) for his highly competent support in the programming of the experimental stimulation. Moreover, we are grateful to two anonymous reviewers for their helpful comments and suggestions.

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APPENDIX A. PRESENTATION OF THE ACQUIRED BEHAVIORAL DATA

A.1. Acquisition phase

The behavioral data of the acquisition phase have no direct relation to the study purposes because included condition effects do not provide a criterion for ideomotor processing. Accordingly, these data were analyzed mainly to confirm that subjects adequately followed the task instructions. Error rate during no-go trials (''false alarms'') was 2.2%. The mean RT was 374 ms, which was identical for both experimental groups. There were slightly more right-hand responses during go trials (50.5% vs. 49.5%) but this difference was far from significant ($t(32) = 0.600$, $p = .543$).

A.2. Test phase

Response frequencies (RF). The analysis of the RFs revealed no statistically significant compatibility effect (left responses: $t(17) = 0.391$; $p = .350$; right responses: $t(17) = 0.241$; $p = .406$; both one-tailed tests for directional hypothesis), even though subjects showed a slight numerical preference for tone-compatible over incompatible responses[5] (left responses: 49.7 ± 5.8% incompatible vs. 50.3 ± 5.8% compatible; right responses: 49.6 ± 4.2% incompatible vs. 50.4 ± 4.2% compatible; values represent mean percentages and respective standard errors).

Reaction time. Descriptively, we observed a non-specific response-facilitation effect through action-effect tones as compared to neutral tones, i.e. responses were faster for both compatible and incompatible tones as compared to trials with the neutral tone. More specifically, left-hand action effects produced faster left-hand and faster right-hand responses compared to neutral tones. This effect was much (three times) stronger for left-hand than for right-hand responses. Right-hand LAEs, on the other hand, accelerated only left-hand but not right-hand responses. For mean reaction times and corresponding standard errors see Table A and Figure A below.

A 3×2 repeated-measures ANOVA revealed a significant main effect for ideomotor tone association [$F(2,34) = 3.347$; $p = .047$] but not for response side [$F(1,17) = 1.968$; $p = .179$], suggesting that perceiving a learned action effect facilitates response selection (cf. Melcher et al., 2008). However, the interaction effect between tone association and response side [$F(2,34) = 0.899$; $p = .416$] did not reach the significance level, which is why we continued with some more progressive post hoc testing. We defined t-contrasts (without correction for multiple testing) to define single effects of response acceleration by LAEs. This revealed a significant facilitation of left-hand but not of right-hand responses through left-hand action effects (contrasts ''neutral tone minus left-hand effect tone'' for left-hand/right-hand responses: $t(17) = 2.153/1.492$; p(one-tailed) = .023/.075). Similarly, right-hand action effects compared to neutral tones accelerated left-hand but not right-hand responses to a significant extent (contrasts ''neutral tone minus right-hand effect tone'' for left-hand/right-hand responses: $t(17) = 1.981/0.193$; p(one-tailed) = .032/.425). Differential findings of *t*-tests for left-hand and right-hand reactions suggest an interaction between ideomotor processing (namely response facilitation by learned action effects) and response-side which, however, is not significant in the omnibus ANOVA and therefore should be interpreted with caution. Taken together, at least at the descriptive level, the data exhibited an interaction effect between response-side and ideomotor condition with increased ideomotor effects for the left side (i.e. left-hand action effects and left-hand actions).

Response	Compatibility relation					
	Compatible		Incompatible		Neutral	
Left	431.8	±21.5	436.4	±22.2	445.0	±22.7
Right	431.6	±18.0	425.7	±19.0	430.7	±18.5
Mean	431.7	±19.4	431.0	±20.4	437.8	±20.3

Table A lists mean reaction times and corresponding standard errors in the different ideomotor conditions of go trials (compatible, incompatible, and neutral), separately for left-hand and right-hand responses. The data exhibits no significant or consistent compatibility effect. Rather, there was general response acceleration for trials in which an action effect stimulus is presented, irrespective of the specific acquired motor association.

[5] The term compatible denotes responses in the test phase which match the acquired response association of the tone signal presented in the current trial: i.e. either a right button press executed after the tone which has been presented following right responses during the acquisition phase, or *vice versa*. Inversely, incompatible responses are opposed to the previously acquired association.

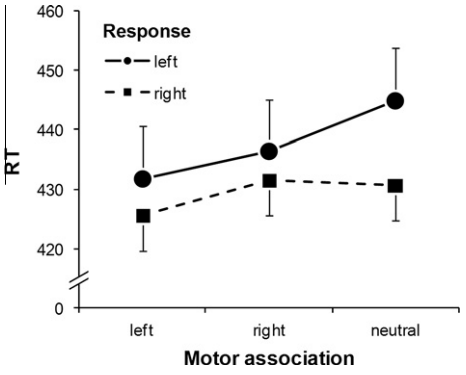

Figure visualizes mean reaction times (in ms) of go trials depending on the acquired motor association of the presented tone stimulus. Lines (descriptively) visualize the effect of response acceleration for tones associated with the left-hand response and tones associated with the right-hand response (compared to neutral/"unassociated" tones), separately for left-hand and right-hand responses. The acceleration effect failed to appear for right-hand responses when the right-hand action effect is presented. Error bars represent 95% within-subject confidence intervals (Loftus, Masson (1994) Psychon Bull Rev 1:476–490), computed separately for left and right responses.

Other than most previous studies that used the two-phase ideomotor learning paradigm, the present work did not exhibit a consistent significant behavioral signature of IRA. This can be plausibly explained by the fact that subjects in the present study did not respond to the action effect stimulus itself. Rather, the action effect stimulus accompanied the imperative visual target stimulus during go trials and thereby had no relevance for either the response selection or execution. This brought the important advantage that we could present action effect stimuli during no-go trials too, i.e. without prompting subjects to execute a proper motor action. Accordingly, we could define brain activations related to the perception of learned action effects in situations in which subjects are passive, so that defined effects of IRA were not confounded with the effects of proper motor actions. This advantage, however, arguably came at the price of diminished behavioral effects which we expected and accepted already in the study planning (cf. Melcher et al., 2008).

APPENDIX B. COMPARISON OF NEUROIMAGING FINDINGS WITH THE MELCHER ET AL. (2008) STUDY

Region	Melcher et al. (2008)		Present study		
	Coordinates	*t* value	Coordinates	*t* value	*k*
R dorsal premotor cortex	48 −12 44	5.55	42 −6 48	3.15	146
L SMA/paracentral lobule (BA 6)	−12 −20 68	5.16	−9 −30 60	4.62	62
L frontopolar cortex	−16 60 −4	4.24	6 54 −6	4.33	54
R (dorsal) postcentral gyrus	28 −28 72	4.06	n.s.		
L anterior intraparietal cortex	−24 −40 56	6.11	−30 −33 54	3.88	368
L temporo-parietal junction	−52 −52 28	6.19	−45 −45 21	4.35	69
L Heschl's gyrus/posterior insula	−44 −12 8	5.35	n.s.		
R Heschl's gyrus/posterior insula	52 −16 8	5.09	[36 −24 9]	3.63	[9243*][a]
L middle temporal gyrus	−48 −4 −20	5.39	n.s.		
R hippocampus/parahippocampal gyrus	24 −40 0	5.90	18 −27 12	3.57	157
L/R midbrain	−4 −4 −8	4.63	n.s.		
L/R cerebellar vermis	0 −52 −12	6.37	6 −51 0	3.58	175
R inferior occipital	44 −88 −8	5.36	[33 −72 0]	3.47	[9243*][a]
L inferior/middle occipital cortex	−24 −88 −4	5.28	[−18 −84 −12]	3.60	41*
L cuneus/calcarine sulcus	0 −80 16	4.22	[3 −81 −12]	4.36	[9243*][a]

[a]Sub-foci of the same cluster.

Table lists brain activations related to IRA in the study of Melcher et al. (2008) (contrast "left-hand LAEs vs. neutral tone") and analogous activations in the present study. The corresponding coordinates represent the nearest local maxima in the analogous contrast (contrast of nogo2 conditions "left-hand LAEs vs. neutral tone"). Activations of the previous study were determined by random effect analyses thresholded at $p < .001$, with a minimum cluster size of 10 contiguous voxels (see Melcher et al., 2008). Analogous activations in the present data were determined by a random effect analysis, with a stepwise threshold of $p < .001$ ($k \geqslant 30$) and $p < .005$ ($k \geqslant 10$). Activations that only occurred at the lowered threshold are enclosed in brackets and related cluster sizes are marked by an asterisk. The comparison illustrates that the overall pattern replicated rather well. More specifically, we found analogous or overlapping activation in the motor system including the right dorsal premotor cortex (which is contralateral to the response associated with action effect) and the cerebellum. Further analogous activations were observed in (para-)hippocampal regions, the TPJ, and

the anterior intraparietal cortex as well as in the Heschl' gyrus, the cuneus, and lateral occipital cortices. Differences in brain activations between the present and the prior study are most probably due to the changed task context, particularly the different timing of the stimulation (presentation of LAEs after the target in the previous study vs. simultaneously presentation in the present work.) and the different response or action modes (free choice responses in the present study vs. forced choice responses in our former work).

(Accepted 13 November 2012)
(Available online 1 December 2012)