NeuroImage

www.elsevier.com/locate/ynimg
NeuroImage 39 (2008) 1274 – 1288

The neural substrate of the ideomotor principle: An event-related fMRI analysis

Tobias Melcher,[a,*] Maaike Weidema,[b] Rena M. Eenshuistra,[b]
Bernhard Hommel,[b] and Oliver Gruber[a]

[a] *Department of Psychiatry and Psychotherapy, Systems Neuroscience Unit, Georg-August-University, Goettingen, von-Siebold-Str. 5, 37075 Goettingen, Germany*
[b] *Leiden University Institute for Psychological Research & Leiden Institute for Brain and Cognition, The Netherlands*

Received 2 June 2007; revised 14 September 2007; accepted 25 September 2007
Available online 10 October 2007

The present fMRI study sought to investigate the neural basis of perceiving learned action effects and thereby to test for hypotheses based on the ideomotor principle. For this purpose, we had subjects undergo a two-phase experimental procedure comprising an acquisition and a test phase, the latter administered inside the MR scanner. During the acquisition phase, free-choice button presses were contingently followed by one of two tones of different pitch which thereby should become "learned action effects". During the following test phase, subjects were presented with the action effects either when in a passive (non-acting) state or when they carried out forced-choice button presses. Conform to our expectations, we found evidence for a motor effector activation following the passive perception of effect tones which elicited activation in the neural motor system (premotor and somatosensory cortices, SMA, and cerebellum). Surprisingly, however, this activation was observed for left-hand effect tones only, suggesting a basic asymmetry in the impact of ideomotor learning. Moreover, we found activation in the posterior prefrontal and temporo-parietal cortex in response to action effects during the pursuit of goal-directed action. This suggests that action effects attracted special attention and thereby engaged selective cognitive control processes to ensure task-appropriate performance. Finally, there was reduced premotor activation for response-compatible as compared to response-incompatible action effects which can be taken as indication for differential requirements on the motor system and thus for behavioral interference and/or facilitation by learned action effects.

Introduction

Carrying out a goal-directed action presupposes knowledge about what that action leads to. This knowledge about the to-be-expected action effects allows the agent to purposefully select among possible movement patterns in order to achieve a given action goal, while a lack of it renders behavior necessarily accidental and ineffective. The important role of acquired associations between motor actions (i.e. movements) and their perceivable sensory effects has been emphasized by the ideomotor (IM) principle. This principle can be traced back to the nineteenth century (James, 1890; Lotze, 1852; Harleß, 1861) but has found its way into more recent theoretical accounts of voluntary action control (e.g. Greenwald, 1970; Prinz, 1987; Hommel, 1996a; Elsner and Hommel, 2001, 2004).

Essentially, IM theories claim that performing a movement and perceiving its consequences leads to the integration of the respective motor pattern and the resulting perceptual codes, referred to as IM learning. IM learning is assumed to be an automatic process that occurs without the agent's intention (i.e. a form of incidental learning) or even outside the agent's awareness (cf. Elsner and Hommel, 2001, 2004; Hommel et al., 2003). Once the agent has acquired the association between a given motor pattern and its perceptual consequences, the representations of these consequences serve as retrieval cues for activating the action intentionally – actions can thus be voluntarily produced by "thinking of" (or anticipating) their effects (James, 1890). This presupposes that associations between motor patterns and acquired action effects are *bi-directional*, i.e. excitable in either direction from motor codes to effect codes (as typical when acquiring the associations) or back from effect codes to motor codes (as typical when employing the associations for intentional control of action).

The existence of spontaneously acquired action–effect associations, and their bi-directional nature, has been demonstrated in numerous behavioral studies (e.g., Hommel, 1996a; Elsner and Hommel, 2001). Typically, experiments on IM learning comprise two phases. In the first, *learning phase*, subjects are expected to acquire novel action–effect associations incidentally, i.e. even though the task does not require attention to, or consideration of the novel action effects. For instance, subjects are asked to carry out a binary choice task with manual key presses, and each key press leads to the presentation of a particular sound, such as a low or high

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* Corresponding author. Fax: +49 551 39 2798.
E-mail address: tobias.melcher@medizin.uni-goettingen.de (T. Melcher).

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doi:10.1016/j.neuroimage.2007.09.049

tone. During the second, *test phase*, the temporal order of action effects and key presses is reversed, so that the previous effects now serve as stimuli to indicate a particular key press. In *compatible* conditions, the mapping of stimuli to response keys heeds the previous key–effect mapping; for instance, if left- and right-hand key presses had produced low- and high-pitched tones in the learning phase, a low tone would now signal a left-hand key press and a high tone a right-hand key press. In *incompatible* conditions, the mapping of stimuli to response keys is reversed, so that a low tone would now signal a right-hand key press and a high tone a left-hand key press. Studies have consistently shown that performance in the test phase is better in compatible than in incompatible conditions, suggesting that subjects had incidentally learned bi-directional action–effect associations (e.g. Hommel, 1996a; Elsner and Hommel, 2001, 2004; Eenshuistra et al., 2004). Although action effects have been investigated mostly in the auditory domain, there are also demonstrations with visual and proprioceptive (electro-cutaneus) action effects (e.g. Ziessler, 1998; Beckers et al., 2002; Hommel, 2004). Moreover, action–effect associations seem to generalize to feature-overlapping stimuli, e.g. stimuli that refer to a same superordinate category or that share common semantic associations (c.f. Hommel et al., 2003). Both types of findings demonstrate the ecological validity and generalizability of the IM principle.

To our knowledge, there is only one neuroimaging study that is directly concerned with the neural representation of learned action effects: a PET study conducted by Elsner et al. (2002). In this study, subjects first underwent a learning phase during which they carried out free-choice (left- or right-hand) key presses that contingently produced particular tones. During the subsequent test phase, brain activity (in terms of rCBF) was measured by means of repeated PET scans during which subjects passively listened to randomly ordered tone sequences. The main dependent variable was the ratio of neutral tones and previous action–effect tones in these sequences, which ranged from 0% to 100% action–effect tones. Accordingly, a parametric statistical model could be used to determine the brain regions exhibiting a positive correlation between the action–effect ratio and the normalized rCBF. The analysis pointed to two brain regions the activation of which varied as a function of this ratio: the right posterior hippocampus and the supplementary motor area (SMA). The observed activation in hippocampus and SMA arguably reflects the retrieval of the learned action–effect association from episodic memory and the consequent backward activation of the respective manual response, respectively.

Even though the finding of Elsner and colleagues provides preliminary evidence for the neural basis of IM learning and its role in action control, this study has a number of methodological limitations that we attempted to overcome in the present investigation. As Elsner et al. point out, the employed parametric design did not include a baseline condition, which may have led to an underestimation of the brain regions involved in IM learning. Moreover, the study assessed brain activations while subjects were passively presented with action effects but not during the pursuit of goal-directed action. Arguably, brain areas involved in IM-based action control are more active during the planning and execution of intentional actions than during passive listening – another reason to suspect that the observations of Elsner et al. may provide a rather conservative assessment of the neural basis of IM processes. Finally, the PET method allowed for only 12 scans, which turned out to provide insufficient statistical power to distinguish between activations related to right- and left-hand motor actions (cf. Elsner et al., 2002).

The present study sought to overcome these limitations by using event-related fMRI. In particular, we wanted to determine (a) the neural substrate of response activation when subjects are passively facing action effects (similar as in Elsner et al's study) and (b) the neural effects of facilitation and interference if subjects are presented with response-compatible and response-incompatible action effects, respectively, during the pursuit of goal-directed action (i.e. the execution of forced-choice motor actions). As regards the first aim, we were particularly interested in effector-specific effects, i.e. effects of the laterality of the stimulus-associated movements (left-hand vs. right-hand motor action).

For these purposes, we adopted the basic structure of Elsner and Hommel's (2001) two-phase experimental design but modified it to make optimal use of fMRI. During an acquisition phase administered outside the MR scanner, subjects performed a simple go/no-go task in which they carried out free-choice (left- or right-hand) button presses that triggered the presentation of a particular, fully contingent (low-pitched or high-pitched) tone. During the following test phase, subjects underwent fMRI during the performance of another go/no-go task that required forced-choice button presses in response to color circles. Most importantly, responses were not to be carried out until an auditory go signal was presented which was either one of the previous (high- or low-pitch) effect tones, or a third (medium-pitch) tone. These tones were (pseudo-)randomly varied, so that they could be compatible or incompatible with the motor action indicated by the color: they were considered compatible with the actions they had followed in the acquisition phase and incompatible with the alternative actions. Trials that included the medium-pitch tone served as neutral or baseline condition. The tones also appeared in no-go trials, to study the impact of action effects in a passive situation, and there were no-go trials that included no auditory signal at all. The described tasks are visualized in Fig. 1 (acquisition phase) and Fig. 2 (test phase); experimental conditions and respective trial numbers of the test phase are listed in the table of Fig. 3.

Based on IM theories (Hommel, 2003) and the findings of Elsner et al. (2002), we had the following expectations: First, we expected to find activation in brain regions that reflect an increased saliency of learned action effects. More specifically, one could expect to find enhanced activation in sensory association areas (particularly in auditory cortices) as reflecting an increased sensory processing of learned action effects as compared to otherwise comparable sensory stimuli as well as in brain regions that are involved in stimulus-driven (i.e. bottom-up) orienting of attention. In this context, the temporo-parietal junction (TPJ) is a candidate region for the processing of learned action effects because this region has been highly consistently related to stimulus-driven attentional orienting and, more specifically, the processing of sensory stimuli of (potential) behavioral relevance (Corbetta and Shulman, 2002; Downar et al., 2000). Second, we expected to find activation in brain regions related to episodic memory, particularly in the hippocampal system, as neural substrate of the mnemonic retrieval of the acquired action–effect association. Third, we expected that the mere perception of learned action effects would activate brain regions which are known to be involved in the control or initiation of manual motor actions (in particular in the SMA, the lateral premotor and somatosensory cortex) as indication for the activation of motor response tendencies (i.e. effector activation). Here we expected that the laterality of the associated movement is reflected in the laterality of the produced brain activation. Finally, we expected to find activation in brain regions that have been related to the processing

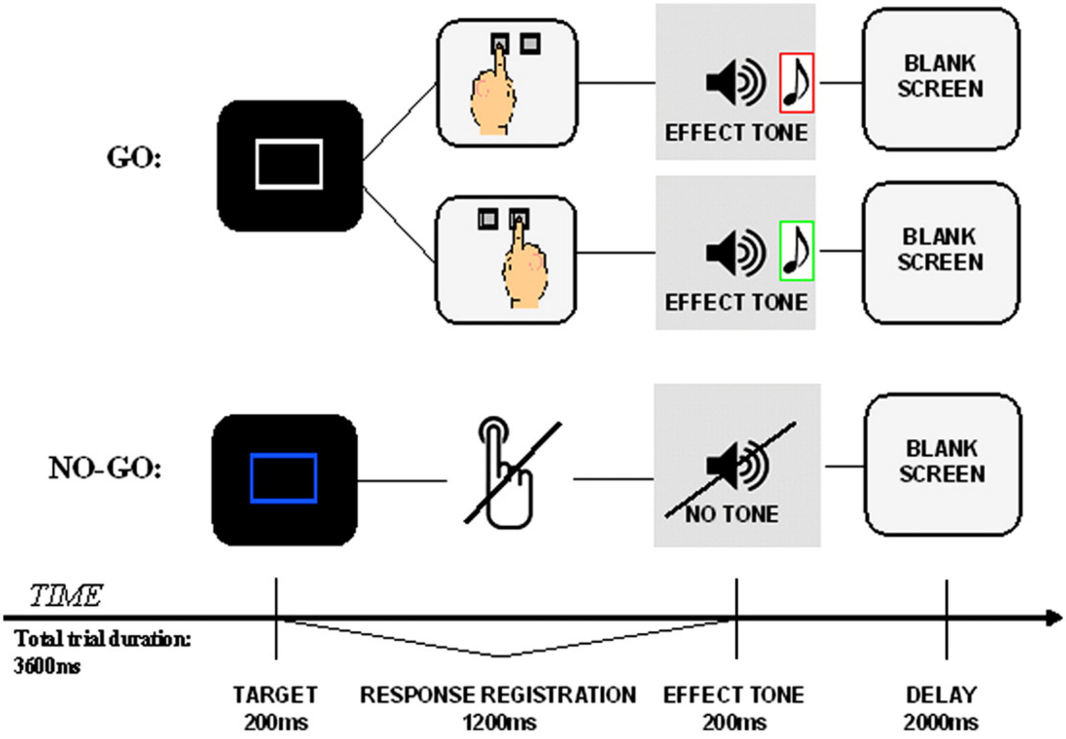


Fig. 1. Task paradigm of the acquisition phase (administered outside the MR scanner): free-choice go/no-go task. Button presses during go trials, indicated by white rectangles, were specifically and contingently followed by tone signals of different pitch (action effects). Blue rectangles indicated no-go trials, i.e. to withhold responding. The different colors (red or green) of the frames around the notes should represent different tone pitches.

of competition and behavioral conflict, such as the dorsal anterior cingulate cortex as well as the dorsolateral and/or anterior ventrolateral prefrontal cortex (cf. Milham et al., 2003; Melcher and Gruber, 2006), if action effects are presented as starting signals for motor actions. In a recent fMRI study, Egner and Hirsch provided key evidence for the assumption that amplification of task-relevant information – in terms of activation boosting in brain regions specialized for the processing of the task-relevant feature information by prefrontal cortices – plays a predominant role in the resolution of cognitive conflict (Egner and Hirsch, 2005). Therefore, we expected to find evidence for amplified color processing especially when incompatible action effects (assumed to induce response conflict) are presented during go trials, which should show up in enhanced activation in extrastriate visual regions known to be involved in color processing, particularly in the lingual gyrus (cf. Corbetta et al., 1991; Zeki and Marini, 1998).

Experimental procedures

Participants

Eighteen healthy and right-handed young adults participated (14 women; mean age 25.61 ± 3.01), after they had given written informed consent. They received monetary payment for participating.

FMRI data acquisition

Imaging was performed on a 1.5-T MRI scanner (Siemens Magnetom Sonata; Siemens Medical Solutions, Erlangen, Germany) with a standard birdcage headcoil. Twenty axial slices (voxel size $3.6 \times 3.6 \times 4$ mm^3, distance factor 0.25) were positioned in parallel to the AC–PC plane, covering the entire brain. Prior to the functional scans, anatomical MDEFT (modified driven equilibrium Fourier transform pulse sequence) slices were obtained. Functional images were obtained during three separated runs of a single-shot, gradient EPI sequence (TR 1.80 s, TE 50 ms, flip angle 90°, filed of view 192 mm, 64×64 matrix) each acquiring a total of 315 image volumes. Events of interest within the experimental course have been systematically jittered in time to achieve an oversampling of the BOLD response (for the exact jittering procedure, see description of the task paradigm below). Using the SPM2 software package (http://www.fil.ion.ucl.ac.uk/spm/), the functional images acquired were realigned, corrected for motion artifacts (SPM2 procedure 'realign and unwrap'), global signal intensity variation, and low-frequency fluctuations (high-pass filter with 128-s cutoff), normalized into the standard stereotactic space (MNI template), and spatially smoothed with a 9-mm full-width at half-maximum Gaussian kernel.

Stimulation and task

The experimental procedure comprised of two phases, an acquisition phase administered outside the MR scanner and a test phase administered during fMRI measurement. In the acquisition phase, subjects performed a mixed two-choice reaction go/no-go task (see Fig. 1). They were presented with white rectangles to indicate a go trial and with blue rectangles to indicate a no-go trial. Go trials required a free-choice button press response with the left-

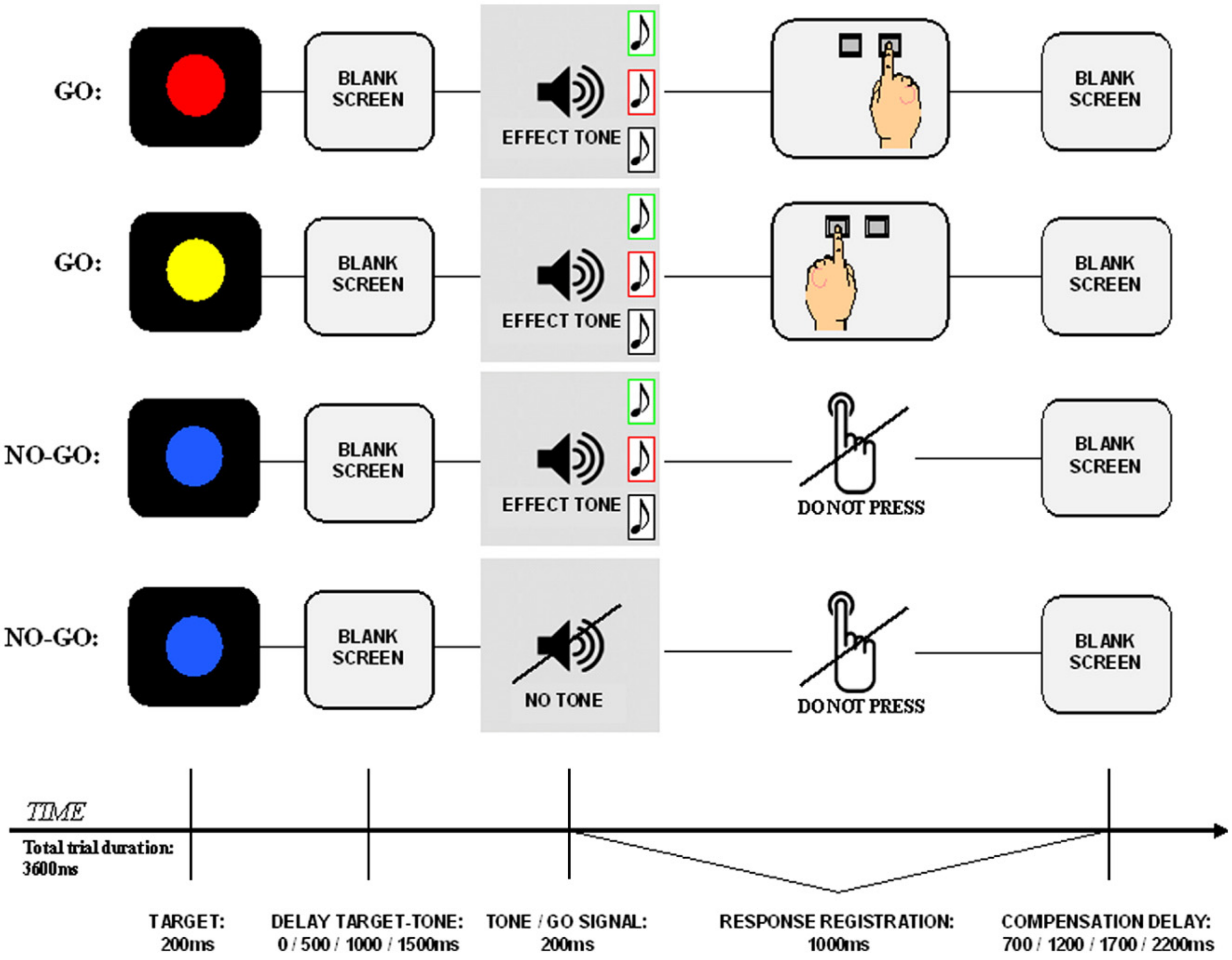
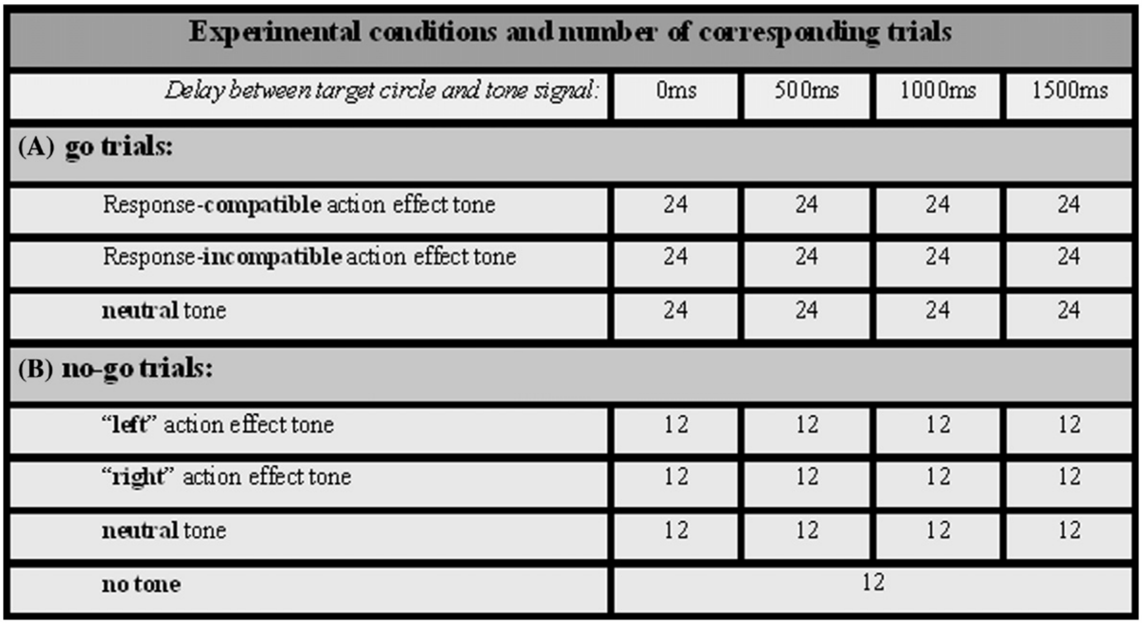


Fig. 2. Task paradigm of the test phase (administered inside the MR-scanner): forced-choice go/no-go task. During go trials, subjects responded to the color identity (red or yellow) of the presented circles. Thereby, subjects did not respond directly but had to wait until the occurrence of an auditory start signal (previous action effect) that followed the targets after a varying delay (ranging from 0 to 1500 ms). Blue circles indicated no-go trials, i.e. to withhold responding. The color (green or red) of the frames around the notes illustrates the response–association of the presented tone according to the response–tone practice during the acquisition phase (black frame represents the neutral tone). On each trial, only one of the three tones was presented.

hand or right-hand index finger. Subjects were asked to press the two buttons in a random, non-systematical order and about equally often. When being pressed, each button produced a particular auditory effect: a 200-ms 261-Hz sinusoidal tone corresponding to a “C0” or 523-Hz sinusoidal tone corresponding to a “C1” one octave above, presented through headphones. Subjects were explained that the tones were not important for the task but would merely indicate that their response was adequately registered. The assignment of tones (high vs. low) to buttons (left vs. right) was counterbalanced across subjects. No-go trials were included to enhance attentional requirements of the task in order to ensure an adequate level of attention. Participants were told to press buttons as quickly as possible in go trials but that it would be equally important to avoid false alarms on no-go trials.

Each trial started with the presentation of a blank screen for 1400 ms, followed by the white or blue target stimulus presented for 200 ms. Responses were registered for 1200 ms from the onset of the target presentation. On go trials, the action effect tone was presented 1000 ms after the offset of the target, if – and only if – a response was given. The total trial length (of both go and no-go trials) was 3600 ms. Each participant performed 255 acquisition trials (204 go trials and 51 no-go trials), administered in three blocks of equal length.

In the test phase, subjects responded to the colored circles by using the same push-button device as during the acquisition phase (see Fig. 2). The assignment of colors (red or yellow) to buttons (left or right) was counterbalanced across subjects. Before giving their response, subjects had to wait for the occurrence of an auditory start signal that consisted of one of the previous effect tones, or a third tone that did not occur during the acquisition phase. The third tone was of medium pitch (370-Hz sinusoidal tone corresponding to a “F#0”), lying exactly halfway between the two effect tones. The combination of colors and tones created three experimental conditions during go trials. With respect to the previous button–tone practice, effect tones could be either compatible or incompatible with the response to be given. On neutral trials, which should serve as baseline condition, the starting signal consisted of the medium pitch tone that bore no response association. Reaction



Experimental conditions and number of corresponding trials				
Delay between target circle and tone signal:	0ms	500ms	1000ms	1500ms
(A) go trials:				
Response-**compatible** action effect tone	24	24	24	24
Response-**incompatible** action effect tone	24	24	24	24
neutral tone	24	24	24	24
(B) no-go trials:				
“**left**” action effect tone	12	12	12	12
“**right**” action effect tone	12	12	12	12
neutral tone	12	12	12	12
no tone	12			

Fig. 3. Experimental design: trial types (experimental conditions) and respective trial numbers during the test phase.

times during go trials were defined as latency of the button press relative to the onset of the auditory go signal. No-go trials – i.e. trials that required withholding responses – were indicated by blue-colored circles. These trials could include one of the action effect tones (either the left-hand or right-hand effect tone), the neutral (i.e. medium pitch) tone, or no tone at all, which provided four further experimental conditions.

The time delay between offset of the target and onset of the auditory start signal was systematically varied ranging from 0 to 1500 ms with an increment of 500 ms. This variation was included for fMRI methodological reasons only – as temporal jitter to increase signal discriminability – and accordingly was not treated as an experimental factor in the statistical analyses. Subjects performed 444 trials of the test task, separated in three blocks (fMRI sessions) of approximately equal length. Go trial conditions (incompatible, compatible and neutral trials) occurred 96 times (24 times for each delay length), each. No-go trial conditions including a left-associated, right-associated, or neutral tone signal occurred 48 times (12 times for each delay length), each, and no-go trials that include no tone signal occurred 12 times (see Fig. 3). The trial order was generated to ensure that every trial type follows every other trial type equally often.

Directly following the acquisition phase, we presented subjects through headphones with the medium-pitch tone appearing in a consecutive sequence (50 times; presentation length 200 ms; SOA 2200 ms) in order to habituate them to it, and hence to avoid neural effects of novelty on neutral trials during the fMRI session. During the tone presentation, subjects were to passively watch a fixation cross that occurred simultaneously with the tone, resting their index fingers on the response buttons. Again, subjects were told that the tone would be irrelevant for the task performance. The stimuli were presented by using ERTS (Experimental Run Time System, Version 3.11, BeriSoft Cooperation, Frankfurt am Main, Germany). Between the two experimental phases (from the end of the acquisition task to the beginning of the test task), there occurred a delay of about 30 to 45 min that involved the way from the test lab to the scanner room, the scanner instruction, the task instruction, and the anatomical scanning.

Data analyses

Behavioral data

Statistical analysis of the behavioral data used SPSS 11.5 for Windows. Reaction times (RTs) and error rates from go trials of the test phase were aggregated across subjects and compatibility conditions, and analyzed by means of a repeated measures analysis of variance (ANOVA; thresholded at $p<0.05$). Paired post-hoc comparisons between conditions (Bonferroni-adjusted for multiple comparisons) were planned to be conducted in case of a significant main effect in order to determine single effects of interference and facilitation.

Neuroimaging data

For the 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. The analysis was based on a least-squares estimation using the general linear model for time-series data on a voxel-by-voxel basis. Contrasts between the different conditions were calculated using the t statistic (one-sample t-test). Contrasts between compatibility conditions for go trials were calculated to elucidate neural effects of interference and facilitation; trials with neutral tones served as baseline condition (contrasts “incompatible vs. neutral”, “compatible vs. neutral”, and “incompatible vs. compatible”). Contrasts between conditions from no-go trials were computed to elucidate neural effects of the “pure” perception of action effects in a passive, non-acting state; trials with neutral tones served again as baseline condition (contrast: “effect tones [collapsed across left and right response associations] vs. neutral tone”, “left-hand effect tone vs. neutral tone”, and “right-hand effect tone vs. neutral tone”). Moreover, we contrasted both left-hand and right-hand effect tones with “no tone” trials (contrasts:

"left-hand effect tone vs. no tone" and "right-hand effect tone vs. no tone"), to make sure that possible activation foci refer to activations related to the effect tones rather than deactivations related to the neutral tone. Finally, we contrasted neutral tones with "no tone" trials in order to determine brain activations that are related to the mere tone perception. This contrast should show which of the activations that distinguish between effect tones and the neutral tone are more qualitative or more quantitative in nature (the latter ones would be also elicited by neutral tones). For group statistics, random effect analyses (Holmes and Friston, 1998) were performed on single subject contrast images, thresholded at $p<0.001$, uncorrected, with a minimum cluster size of 10 contiguous voxels.

Results

Behavioral data (test phase/go trials)

Trials with missing go responses (1.8 %) were excluded from further analysis. The overall error rate (ER) amounted to 5%, which was rather evenly distributed across the different conditions (compatible 5%, incompatible 5%, neutral 4%). Accordingly, the error analysis (chi-square test) was far from significant ($\chi^2=0.759$; $p=0.684$). For the RT analyses, error trials were excluded. Mean RT was also virtually identical across the experimental conditions [means ± standard error: compatible 392 ms ± 23.2; incompatible 389 ms ± 22.1; neutral 390 ms ± 21.4]. Accordingly, the analysis (repeated measures ANOVA) revealed no significant effect [$F(2,17)=0.481$, $p=0.622$], and no post-hoc tests were conducted. Thus, RTs and ERs showed no effect of response compatibility of the presented action effect tones. In a second step, we looked whether an effect of response-compatibility might be covered (i.e. modulated) by another factor, such as time (i.e. phase of the experimental course) or side (i.e. handedness) of the associated motor action, but none of the analyses revealed a significant effect of response compatibility.

Neuroimaging data

No-go trial activations: effects of passively perceiving learned action effects

Pooled effects of left-hand and right-hand effect tones. Action–effect tones compared to neutral tones during no-go trials (contrast: "effect tones vs. neutral tone"; see Fig. 4) elicited three foci of significant activation which were located in the right posterior hippocampus (partially extending into parahippocampal regions and thalamus) (MNI coordinates: 24 −40 0; $t=4.92$; $k=20$), in the cerebellum, namely the cerebellar vermis (MNI coordinates: −4 −52 −16; $t=4.68$; $k=21$), and in the left inferior and middle occipital cortex extending into the lingual gyrus (MNI coordinates: −20 −88 −4; $t=4.43$; $k=23$).

Specific effects of left-hand and right-hand effect tones (effector-specific effects)

Left-hand effect tones. Left-hand effect tones considered separately (contrast: "left-hand effect tone vs. neutral tone"; see Table 1; Figs. 5 and 6) were related to significant activation in the right precentral gyrus belonging to the dorsal premotor cortex and in the left supplementary motor area (SMA). Moreover, there was one activation cluster medially centered in the cerebellar vermis which extended into right ventromedial occipital regions (lingual gyrus and cuneus) and also into the right inferior occipital cortex. In the contralateral (left) hemisphere, there was likewise significant activation in the inferior/middle and medial occipital cortex. Furthermore, there was an extended activation cluster that peaked in the left temporo-parietal cortex, in the so-called temporo-parietal junction (TPJ). Further sub-foci of this cluster were located more anteriorly in the (left) transverse temporal (Heschl) gyrus and posterior insula. The latter activation cluster was conjoint with another cluster that peaked in the (left) middle temporal gyrus. There was also activation in the transverse temporal (Heschl) gyrus in the right hemisphere. Moreover, there was significant activation in the right posterior hippocampus, partially extending into the parahippocampal cortex, and in the right superior postcentral gyrus. Finally, there was significant activation in the left midbrain, in the left frontopolar cortex and in the left anterior intraparietal cortex at the intersection of postcentral and intraparietal sulcus.

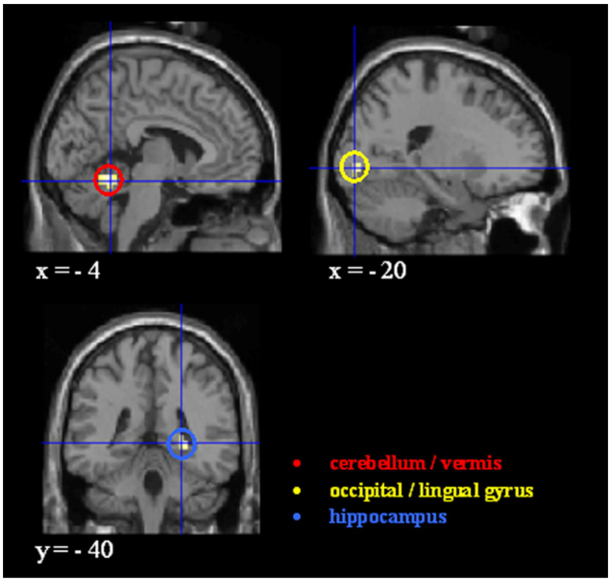


Fig. 4. Brain activations related to the perception of action effect tones (contrast: "effect tones vs. neutral tone"). Depicted activations were rendered onto cross-sectional (sagittal, coronal, and axial) slices of the anatomic MNI template, thresholded at $p<0.001$ with a minimum cluster size of 10 contiguous voxels.

All activations of the contrast "left-hand effect tone vs. neutral tone" were also present in the contrast "left-hand effect tone vs. no tone" (see Table 1) confirming that the revealed activation foci reflect proper signal increases related to effect tones rather than deactivations related to neutral tones. The contrast "neutral tone vs. no tone" revealed also significant activation in the (bilateral) primary auditory cortex and the cerebellar vermis suggesting that the differences between left-hand and neutral tone in these regions are "only" quantitative (rather than qualitatively) in nature. The inverse contrast ("neutral tone vs. left-hand effect tone") revealed no suprathreshold activation, conforming that neutral tones provide an adequate baseline condition.

Right-hand effect tones. Right-hand effect tones (contrast: "right-hand effect tone vs. neutral tone") exhibited no significant activation at the set statistical threshold. Compared to no-tone trials (contrast: "right-hand effect tone vs. no tone"; see Table 2), right-hand effect tones exhibited significant activation in a more ventral region of the SMA (i.e. the cingulate motor area (CMA)), in the

Table 1
Activations during no-go trials associated with the perception of left-hand effect tones, in comparison with activations related to neutral tones

Region	no-go_left vs. no-go_neutral		*k*	#	no-go_left vs. no-go_notone		no-go_neutral vs. no-go_notone		no-go_neutral vs. no-go_left
	Coordinates/ statistical effect				Coordinates/ statistical effect		Coordinates/ statistical effect		Coordinates/ statistical effect
R dorsal premotor cortex	48 −12 44	5.55	67	1	40 −20 40	6.37	n.s.		No suprathreshold clusters
					60 −12 48	5.85			
L dorsal premotor cortex	n.s.				−52 −12 52	5.03	[−52 −12 52][a]	2.96	
L/R SMA	−12 −20 68	5.16	10	2	−8 −16 48	7.11	n.s.		
					8 −24 72	5.78			
L frontopolar cortex	−16 60 −4	4.24	10	3	[−28 40 −4][b]	3.69	n.s.		
R (dorsal) postcentral gyrus	28 −28 72	4.06	13	4	28 −36 64	13.18	n.s.		
L anterior intraparietal cortex	−24 −40 56	6.11	37	5	−20 −36 56	4.42	n.s.		
L temporo-parietal junction	−52 −52 28	6.19	253	6	−52 −44 24	5.83	n.s.		
L Heschl’s gyrus/posterior insula	−44 −12 8	5.35	253	6	−52 −28 8	10.49	−48 −28 8	7.98	
R Heschl’s gyrus/posterior insula	52 −16 8	5.09	39		64 −12 8	11.84	56 −16 8	8.82	
					44 −28 8	7.88			
L middle temporal gyrus	−48 −4 −20	5.39	253	6	−48 −4 −20	5.16	n.s.		
R hippocampus/parahippocampal gyrus	24 −40 0	5.90			20 −28 −4	5.81	n.s.		
L hippocampus	n.s.	n.s.			−32 −16 −12	7.90	−32 −16 −8	5.51	
L/R midbrain	−4 −4 −8	4.63	22	7	8 −12 −8	3.77	n.s.		
L/R cerebellar vermis	0 −52 −12	6.37	309	8	8 −52 −20	4.33	−12 −48 −4	4.77	
R inferior occipital	44 −88 −8	5.36	309	8	32 −84 −12	4.33	n.s.		
L inferior/middle occipital cortex	−24 −88 −4	5.28	71	9	−8 −88 8	3.73	n.s.		
L cuneus/calcarine sulcus	0 −80 16	4.22	309	8	−4 −88 36	4.35	n.s.		
L lingual gyrus	n.s.				−16 −48 −8	5.78	n.s.		
Brain stem	n.s.				0 −20 −16	6.06	n.s.		

Contrasts: “left-hand effect tone vs. neutral tone”, “left-hand effect tone vs. no tone”, “neutral tone vs. no tone”, and “neutral tone vs. left-hand effect tone”. All activations were determined by random effects analyses on single-subject contrast images, thresholded at $p<0.001$, with a minimum cluster size of 10 contiguous voxels. The table relates the reported activation foci to activation clusters (see numbers in column ‘#’) in order to point out which of the foci refer to common clusters.

n.s. = not significant. *k* = cluster size (number of voxels). # = cluster number.

[a] Lowered threshold: $p>0.005$.

[b] Lowered threshold: $k>2$.

posterior bank of the central sulcus (postcentral gyrus), in the bilateral Heschl gyrus, and in the left hippocampus. All mentioned activations were also present in the contrast “neutral tone vs. no tone” (albeit partially not satisfying the voxel criterion of $k \geq 10$; see Table 2) which explains the lack of significant activation in the direct comparison of right-hand tones and neutral tones.

Go trial activations: effects response-compatible and response-incompatible effect tones during the execution of forced-choice motor responses

Interference effects emanating from response-incompatible effect tones. To define effects of interference by response-incompatible effect tones, we computed the contrasts “incompatible vs. neutral” and “incompatible vs. compatible” (see Table 3a/b; Figs. 7a, b and 8). Incompatible trials contrasted with neutral trials showed significant activation in the right posterior PFC comprising the so-called inferior frontal junction (IFJ), and in the left posterior PFC (posterior inferior frontal sulcus) comprising of both the frontal operculum and the IFJ. Moreover, there was bilateral significant activation in the vicinity of the posterior superior temporal sulcus, in the temporo-parietal cortex or junction (TPJ). Finally, the contrast revealed a cluster of significant activation that comprised the left transverse temporal (Heschl’s) gyrus and posterior insula.

Moreover, incompatible trials contrasted with compatible trials exhibited significant activation in the right precentral gyrus, a region belonging to the premotor cortex, and in the SMA. Moreover, there was significant activation in the right transverse temporal (Heschl) gyrus and in the basal ganglia (putamen).

Facilitation effects of response-compatible effect tones. To determine potential facilitation effects emanating from response-compatible effect tones, we computed the contrast “compatible vs. neutral” (see Table 3c and Fig. 7c). This contrast revealed no significant activation at the given statistical threshold. After slightly lowering the statistical threshold to $p<.005$ ($k \geq 10$), which can still be considered a reliable criterion (Forman et al., 1995), there was significant activation in the left posterior PFC (IFJ), left inferior and middle temporal gyrus, and in the left temporo-parietal cortex (TPJ).

Discussion

(Absence of) behavioral effects

We did not find significant behavioral priming effects during go trials, neither in terms of facilitation by response-compatible effect tones, nor in terms of interference by response-incompatible effect tones. This lack of priming effects might not be especially surprising as it can be well explained – or even expected – by the structure of the applied task paradigm that deviates from Elsner and Hommel’s original task quite a bit. In particular, turning the original speeded–reaction binary-choice task into a go/no-go task brought advantages

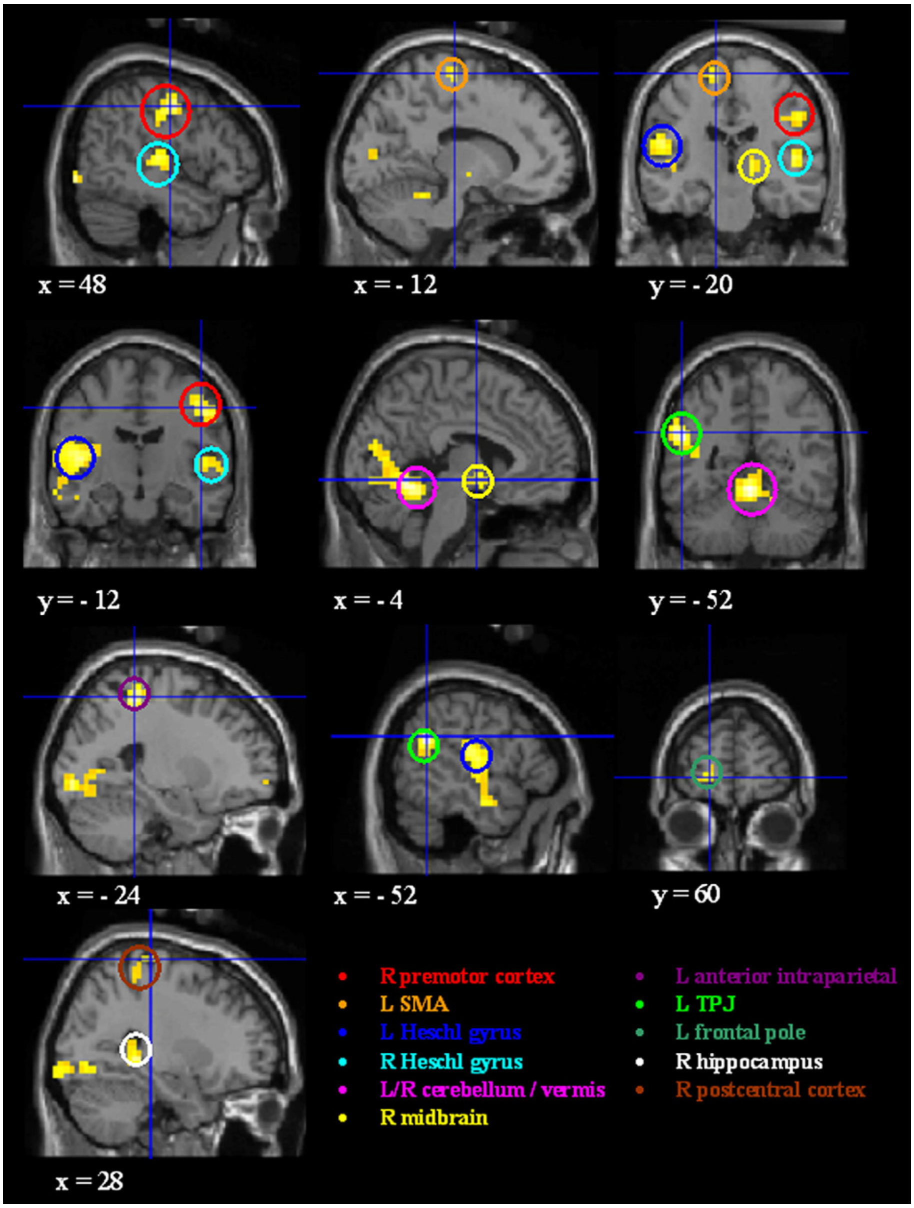


Fig. 5. Brain activations related to the perception of left-hand effect tones (contrast: “left-hand effect tone vs. neutral tone”). Depicted activations were rendered onto cross-sectional (sagittal, coronal, and axial) slices of the anatomic MNI template, thresholded at $p < 0.001$, with a minimum cluster size of 10 contiguous voxels.

and disadvantages with it. Most importantly, identifying the response before the go signal helped us to separate response selection and response execution in time, so to produce purer fMRI signals, and the use of no-go signals allowed us to assess the impact of action effects on response selection without confounding activations from response execution. On the other hand, the disadvantage of this modification is that it works against behavioral effects. Compatibility effects impact response selection (Kornblum et al., 1990) and thus show up in reaction times and choice errors more the greater response uncertainty is (Hommel, 1996b). Informing subjects about the action before presenting a go signal gives them the opportunity to select the response already (i.e., to resolve response uncertainty almost entirely), with the consequence that compatibility effects are relatively unlikely to affect the reaction time to the go signal. Accordingly, our behavioral data alone provide no indication for the occurrence of IM learning during the acquisition phase. Even though this is a disadvantage, previous studies provided ample evidence for the existence of IM learning and our fMRI data are fully consistent with the previous behavioral observations.

Moreover, in the present study’s acquisition phase, the delay between button press and the to-be-learned action effects (i.e. tone signals) was relatively long as compared to prior IM experiments (cf. Elsner et al., 2002; Elsner and Hommel, 2004). As the strength of acquired associations between actions and action effects decreases with a decreasing temporal contiguity of the respective experimental events (cf. Elsner and Hommel, 2004), this may have also contributed to some extent to the fact that learned action–effects had no behavioral correlate in the current data.

Based on the lack of a significant behavioral priming effect, we conducted additional fMRI data analyses to correlate effects in the

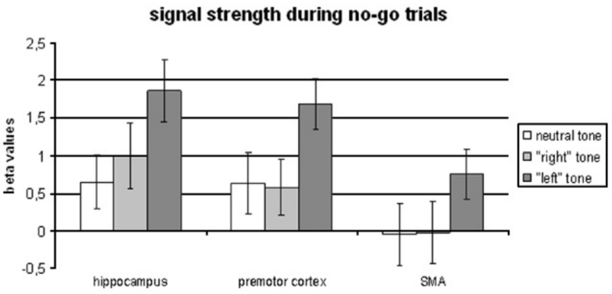


Fig. 6. Activation strengths during no-go trials: bar chart depicts mean beta values and correspondent standard errors in different regions of interest (ROIs). ROIs were defined by using a 10-mm sphere around peak activations (i.e. voxels) from the random effects analyses serving as center. More specifically, we defined three ROIs that all refer to activations of the contrast "left vs. neutral" which were the right dorsal premotor cortex (center coordinates: 48 −12 44), the SMA (center coordinates: −12 −20 60), and the hippocampus (center coordinates: 24 −40 0). Both ROI definition and the extraction of beta values from the GLM used marsbar 0.38.2.

Table 3
Activations associated with response-compatible and response-incompatible effect tones during go trials

Region	Coordinates	*t* value	*k*
(a) Incompatible vs. neutral			
R ventroposterior PFC/IFJ	48 8 28	5.87	69
L ventroposterior PFC/IFJ/ frontal operculum	−56 16 12	4.24	26
L posterior insula/Heschl	−28 −28 20	5.20	14
R TPJ/superior temporal	52 −60 12	4.64	50
L TPJ/inferior parietal cortex	−48 −52 24	4.34	21
(b) Incompatible vs. compatible			
R superior frontal/SMA	16 −12 72	6.36	15
R precentral sulcus/premotor cortex	60 4 36	5.40	23
R Heschl/primary auditory cotex	40 −32 12	4.49	15
L basal ganglia (putamen)	−28 −16 20	5.31	15
(c) Compatible vs. neutral			
L precentral sulcus/premotor cortex/IFJ	[−36 −4 32] [a]	4.32	22
L middle temporal gyrus	[−64 −40 −4] [a]	4.45	28
L temporo-parietal cortex	[−56 −48 24] [a]	3.24	10

Contrasts: "incompatible vs. compatible", "incompatible vs. neutral", and "compatible vs. neutral". All activations were determined by random effects analyses on single-subject contrast images, thresholded at $p<0.001$, with a minimum cluster size of 10 contiguous voxels. For the contrast "compatible vs. neutral", the statistical threshold was slightly lowered to $p<0.005$ (due to lack of significant activations at $p<0.001$).

k=cluster size (number of voxels).

[a] Lowered threshold: $p>0.005$.

RT data (i.e. mean RT differences) with activations in the respective fMRI contrasts. More specifically, we set up three random effect models (SPM model "simple regression") that relate activations of the contrasts "incompatible vs. compatible", "incompatible vs. neutral", and "compatible vs. neutral" to the respective behavioral effect (mean RT differences in the single subjects' data). Results (i.e. activations) were masked with the basic contrast's activations and thresholded at $p<0.001$, uncorrected. The regression models for the contrasts "incompatible vs. neutral" and "compatible vs. neutral" revealed no significant results. The regression model for the contrast "incompatible vs. compatible" revealed a significant correlation between behavioral effect and activation strength in the SMA (MNI coordinates: 16 −8 72; t=4.06, k=2). In other words, when RTs of incompatible trials increased relative to those of compatible trials, then there was stronger recruitment of the SMA. This finding suggests that – even though not indicated by the statistical comparison of mean RTs – incompatible and compatible trials impose differential requirements on the neural motor system that can be construed in terms of response facilitation and/or response conflict.

The neural substrate of perceiving learned action effects

The neuroimaging findings clearly indicate that perceiving effect tones was different from perceiving (otherwise comparable) neutral tones and thereby elicited significant activation in brain regions conforming to our prior hypotheses. The latter assertion is true for both go trials and no-go trials. Hence, the data confirm that ideomotor learning has occurred during the acquisition phase and also suggest that the neural substrate of perceiving learned action effects may be reliably determined even in the absence of significant behavioral results.

Replication of prior findings

The current work relates to and builds upon the prior PET study of Elsner and colleagues (2002), who found circumscribed activation under passive perception of learned action effects in two regions: the right posterior hippocampus and the SMA. As

Table 2
Activations during no-go trials associated with the perception of right-hand effect tones, in comparison with activations related to neutral tones

Region	no-go_right vs. no-go_notone		no-go_right vs. no-go_neutral	no-go_neutral vs. no-go_notone		no-go_neutral vs. no-go_right
	Coordinates/ statistical effect		Coordinates/ statistical effect	Coordinates/ statistical effect		Coordinates/ statistical effect
R postcentral gyrus/central sulcus (post. bank)	36 −24 44	5.97	No suprathreshold activation	[32 −16 44] [a]	4.04	No suprathreshold activation
L SMA/cingulate motor area	−8 −12 44	4.06		[−8 −4 52] [a]	3.78	
L Heschl's gyrus/posterior insula	60 −16 4	10.49		−48 −28 8	7.98	
R Heschl's gyrus/posterior insula	−48 −24 8	8.46		56 −16 8	8.82	
L hippocampus	−32 −24 −8	5.13		−32 −16 −8	5.51	
L/R cerebellar vermis	[−8 −52 −8] [a]	3.92		−12 −48 −4	4.77	

Contrasts: "right-hand effect tone vs. neutral tone", "right-hand effect tone vs. no tone", "neutral tone vs. no tone", and "neutral tone vs. right-hand effect tone". All activations were determined by random effects analyses on single-subject contrast images, thresholded at $p<0.001$, with a minimum cluster size of 10 contiguous voxels.

[a] Lowered statistical threshold: $k<10$.

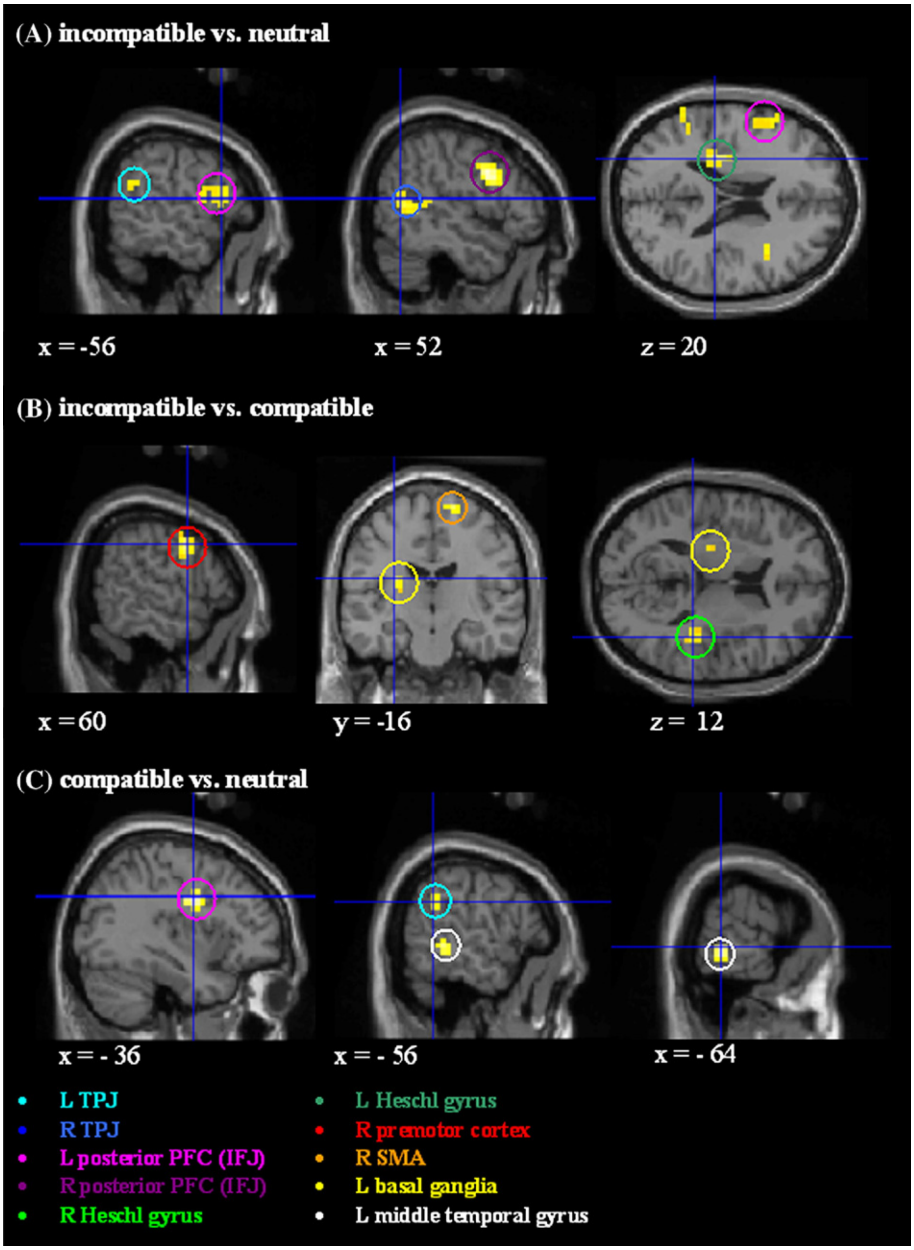


Fig. 7. Brain activations associated with response-compatible and response-incompatible effect tones during go trials. Contrast: "response-incompatible vs. response-compatible", "response-incompatible vs. neutral", "response-compatible vs. neutral". Depicted activations were rendered onto cross-sectional (sagittal, coronal, and axial) slices of the anatomic MNI template, thresholded at $p<0.001$, with a minimum cluster size of 10 contiguous voxels. For the contrast "compatible vs. neutral", the statistical threshold was slightly lowered to $p<0.005$ (due to lack of significant activations at $p<0.001$).

expected, our study replicated both findings. Significant hippocampal activation was found for both (left-hand and right-hand) effect tones taken together (i.e. pooled effect) and for left-hand effect tones alone, while activation in the SMA was exclusively present when we considered left-hand effect tones separately. The hippocampus is well known to be involved in relational episodic memory binding and associative learning (e.g. Brasted et al., 2003; for review see Cohen et al., 1999; Eichenbaum, 2004), including sensorimotor mapping (e.g. Murray and Wise, 1996). Regarding the SMA, it is widely accepted that this brain structure is importantly involved in the observation, imagination, preparation and execution of limb movements, particularly finger and hand movements (e.g. Tyszka et al., 1994; Stephan et al., 1995; Cunnington et al., 2006). In agreement with Elsner and colleagues, we assume that the two activation foci underlie the mnemonic retrieval of episodic action–effect associations and the consequent backward activation of the respective finger movement (i.e. button press).

Plausibility of the other findings

Further activations indicating motor effector activation by learned action effects. While in the study of Elsner and colleagues the hippocampus and SMA were the only regions that exhibited a significant signal increase, we found a series of further significant activations in relation to the perception of learned action effects.

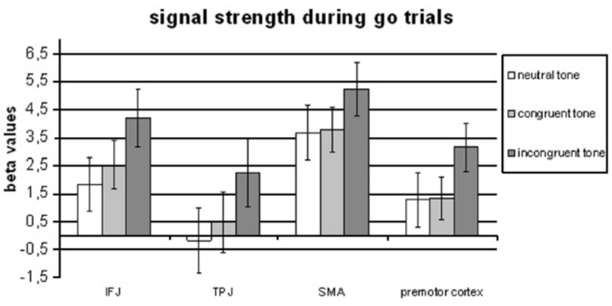


Fig. 8. Activation strengths during go trials: bar chart depicts mean beta values and correspondent standard errors in different regions of interest (ROIs). ROIs were defined by using a 10-mm sphere around peak activations (i.e. voxels) from the random effects analyses serving as center. More specifically, we defined ROIs for the activations in the SMA (center coordinates: 16 −12 72) and in the right premotor cortex (center coordinates: 60 4 36) that have been both revealed by the contrast “incompatible vs. compatible”, as well as for the activations in the right IFJ (center coordinates: 48 8 28) and right TPJ (center coordinates: −48 −52 24) that have been both revealed by the contrast “incompatible vs. neutral”. Both ROI definition and the extraction of beta values from the GLM used marsbar 0.38.2.

This supports our assumption that the method used by Elsner and colleagues might have provided a rather conservative assessment and picked up only the strongest and most robust neural contributions to IM-based response activation. In the present, apparently more sensitive assessment, we observed that the presentation of the left-hand effect tone (contrast “left-hand effect tone vs. neutral tone”) further triggered significant activation particularly in the right dorsal premotor cortex (BA 6) and somatosensory cortex as well as in the cerebellum, i.e. in regions known to play an important role in action control. A comprehensive series of studies found activation in the dorsal premotor cortex related to the performance of (two-)finger movement tasks (e.g. Fink et al., 1997, Cunnington et al., 2006). More specifically, dorsal premotor involvement was repeatedly reported for finger movement preparation with temporally sustained (so-called ‘set-related’) activation during preparation periods after the presentation of instructive cues (Kurata et al., 2000; Wise et al., 1996). Moreover, it has been shown that the imagery and observation of (finger) movements activates the dorsal premotor cortex in a somatotopically specific manner while imagery-related activation seems to spatially coincide with dorsal premotor cortex activation related to the proper execution of the respective movement (Ehrsson et al., 2003; Buccino et al., 2001). Taken together, the reported findings strongly suggest that the dorsal premotor cortex reflects and specifically codes for motor intention, i.e. the preparation of forthcoming movements in terms of effector activation, independent of the ultimate motor execution (cf. Grafton et al., 1998). Evidence for the assumption that the dorsal premotor cortex activation in the current data indeed reflects IM effector activation (i.e. the activation of the button press associated with the tone) is additionally provided by its location in the left hemisphere, contralateral to the respective IM-associated motor action.

The activation in the dorsal somatosensory cortex (i.e. superior postcentral gyrus) was contralateral to the tone-associated finger press response as well. Other studies implicated the same or adjacent regions in hand or finger movements, both when subjects effectively performed movements and when movements were only imagined or illusionary (e.g. Okuda et al., 1995; van Westen et al., 2004; Naito et al., 2002; Michelon et al., 2006). Similarly, the dorsal somatosensory cortex has been repeatedly described as being part of the cortical network that generates the (motor) readiness potential (e.g. Arezzo et al., 1977; Ikeda and Shibasaki, 1992; Urbano et al., 1996). Furthermore, as revealed by morphological investigations of the animal brain (e.g. Huerta and Pons, 1990; Porter, 1991, 1997), the somatosensory cortex projects to primary motor areas and in this way may essentially contribute to the preparation and execution of movements (c.f. Pleger et al., 2006). The cerebellar vermis also represents a brain structure that is primarily related to motor functioning and in particular has been shown to be consistently involved in the mental imagery and execution of finger movements (e.g. Deiber et al., 1998; Lutz et al., 2000; Boecker et al., 2002). Taken together, the activation in the right dorsal premotor and somatosensory cortex as well as in the cerebellum provide further and strong evidence for the assumption that the presentation of the left-hand effect tone has led to a direct motor effector activation, i.e. activation of the corresponding finger movement (left button press).

Enhanced saliency and increased attentional processing of learned action effects. Besides motor-related brain regions, the presentation of (left-hand) effect tones elicited significant activation in the temporo-parietal cortex, i.e. in the so-called temporo-parietal junction (TPJ). The TPJ has been described as key region of a ventral fronto-parietal network that is responsible for bottom-up orienting of attention (Corbetta and Shulman, 2002). More specifically, a comprehensive series of neuroimaging studies suggests that the (bilateral) TPJ importantly contributes to a neural mechanism for detecting sensory features of the environment that are of (potential) behavioral relevance, i.e. that indicate or require some motor response (Downar et al., 2000; Downar et al., 2001; Bledowski et al., 2004). Accordingly, and confirming our expectations, the TPJ activation in the current data suggests that (left-hand) effect tones were more salient and have attracted more attention as compared to neutral tones and, moreover, thereby were processed or evaluated as (potentially) behaviorally relevant events whereas neutral tones were not or, at least, to a lesser degree. The assumption of increased attentional processing is substantiated by the strong activation in the bilateral auditory cortex (Heschl gyrus) related to effect tones. Attentional processing within a specific sensory modality is known to evoke enhanced brain activity in the modality-specific and/or stimulus-feature-specific processing region (Jancke et al., 1999; Kastner and Ungerleider, 2000). Hence, the auditory cortex activation clearly indicates more intense sensory processing of effect tones compared to neutral tones.

Moreover, we found significant activation in relation to action effects in the occipital–visual cortex which may be astonishing – at least at first glance – as the critical experimental manipulation was implemented in the auditory domain and the visual stimulation was counterbalanced across conditions. However, neuroimaging studies clearly indicate that activity in one sensory system can be altered by activity in other sensory systems, while such cross-modal interactions can be both excitatory and inhibitory (cf. Laurienti et al., 2002; Baier et al., 2006). Macaluso et al. (2000) demonstrated that tactile stimulation can enhance activity in the visual system, and Mayer et al. (2006) found activation within the visual system in relation to auditory (re-)orienting. Taken together, findings suggest that orienting responses in one sensory modality can also engage other sensory systems which may explain that effect tones in our experiment elicited activation in the visual–occipital cortex. Generally, the notion that auditory orienting responses also engage the visual system (and vice versa) appears plausible as orienting responses in "real life" (i.e. outside the psychological lab) are commonly (and should be) polysensory.

Besides stimulus-driven attentional processing, the TPJ has been consistently implicated in motor cognition as well as body and self processing which provides an alternative interpretation of the TPJ activation in the current study. In particular, the TPJ is widely considered a key neural structure underlying the experience of 'sense of agency' which is the feeling of being causally involved in or being in control of an action. Farrer and collaborators (e.g. Farrer et al., 2003; Farrer and Frith, 2002), for instance, repeatedly observed increased activity in the right TPJ when subjects attributed an action to another agent, as compared to self-attribution conditions. In pathological conditions, it has been shown that abnormal activity in the TPJ leads to passivity phenomena, i.e. the feeling that one's own actions are externally induced or controlled (e.g. Spence et al., 1997). While the majority of studies implicate the right TPJ in the attribution of agency, there are also reports of left TPJ involvement (e.g. Decety et al., 2002; Chaminade and Decety, 2002). Based on these prior findings, one may speculate that the TPJ activation associated with the perception of learned action effects in the current study reflects the subjects' experience that emerging response tendencies were relatively more externally driven (i.e. by learned action effects) and less dependent on own intentions or goals. This explanation appears especially reasonable given that effect tones were presented arbitrarily, independent of the subjects' initiative or intention.

Effector specificity

In order to confirm actual effector activation by learned action effects, we looked separately for activations related to left-hand and right-hand effect tones. Real effector activation should be reflected in the lateralization of brain activation, i.e. in a right-lateralized activation pattern for left-hand effect tones (i.e. activation in the right premotor and/or somatosensory cortex), and vice versa. The data confirmed effector activation for left-hand action effects with significant activation in the SMA, the right dorsal premotor and somatosensory cortex, as well as in the cerebellum. However, no according activation was found for right-hand action effects in the left hemisphere, which means that right-hand action effects exhibited no activation that goes beyond the activations elicited by neutral tones. In other words, the data provided evidence for direct effector activation only for left-hand action effects, i.e. effects of movements with the subjects' non-dominant hand (all subjects were right-handers). This finding suggests a basic asymmetry in ideomotor learning, i.e. that ideomotor processes may be modulated by the effector side and/or by the agent's handedness. Alternatively, one may also consider that it is not the ideomotor process itself that is modulated by the effector side or the agent's handedness but only the strength of the underlying cortical involvement. More specifically, functional neuroimaging studies on motor execution suggest that motor actions that are performed relatively less proficiently, i.e. that are more complex/difficult or executed with the agent's non-dominant hand, elicit stronger activation in the neural motor system (cf. Kawashima et al., 1993; Dassonville et al., 1997; Lotze et al., 2000; Hammond, 2002). Accordingly, it is conceivable that the backward activation of relatively less automated motor actions by their perceivable effects is also associated with relatively stronger brain activation (as compared to the backward activation of more versed or automated movements) which could account for the stronger impact of left-hand action effects in the current data that was collected in a right-handed subject group. Generally, the found asymmetry raises the question as to whether a group of left-handed subjects would have produced an inverse pattern of results with a strong effect for right-hand action effects and a substantially weaker (or even absent) effect for left-hand action effects. Furthermore, the findings lead to speculate that studies that report significant behavioral priming effects may include an undetected modulation effect by response-side in their data.

The neural substrate of motor interference and facilitation by learned action effects

During go trials, both response-compatible and response-incompatible trials elicited significant activation in the TPJ and IFJ (compatible trials at a slightly lowered statistical threshold). The activation in the TPJ is very similar to the activation elicited by effect tones during no-go trials which we have interpreted as reflecting attentional capture by or increased saliency of action effect tones compared to neutral tones. In roughly the same sense, we presume that TPJ involvement during go-trials underlies an increased processing of those start signals that consisted of effect tones and that, due to their acquired motor association, have attracted enhanced attention. In other words, we presume that the common TPJ activation during incompatible and compatible trials basically reflects that start signals consisting of effect tones provide competing response-associated information of potential behavioral relevance beyond their role as response trigger (cf. Downar et al., 2001). Generally speaking, the presence of competing response-associated information requires agents to re-activate task rules – in our case to respond to color – and to actively select between the competing information streams for response selection (cf. Desimone and Duncan, 1995; Braver et al., 2001; Milham et al., 2003). The IFJ, which was activated by both compatible and incompatible trials, is a candidate region to underlie both of these cognitive functions (cf. Brass et al., 2005; Gruber et al., 2006; Melcher and Gruber, 2006). Therefore, the IFJ activation suggests that, even in the absence of behavioral priming effects, both compatible and incompatible effect tones effectively provided competing – and in the case of incompatible tones also conflicting – response-related information and thus engaged cognitive control processes to ensure task-appropriate performance.

Besides common activation, incompatible trials showed significantly stronger activation as compared to compatible trials in the SMA and in the right premotor cortex. Because response association in the presented tones was counterbalanced in this contrast (compatible and incompatible tones bear equivalent motor associations), these activations cannot be attributed to motor effector association *per se* as this was done in the contrasts of the no-go conditions. Rather, the activation here may reflect that compatible and incompatible trials require a different degree of motor control due to interference and/or facilitation by the presented action effect tones. Since incompatible trials compared to neutral trials revealed no significant activation in the SMA or premotor cortex, the activation in the contrast "incompatible vs. compatible" arguably reflects reduced activation (a relative deactivation) in compatible trials. This, in turn, suggests that the activation in SMA and premotor cortex in the contrast "incompatible vs. compatible" emanates from response facilitation during compatible trials rather than interference during incompatible trials. Of note, the activation clusters in SMA and premotor cortex were located in distinct areas for go and no-go trials which further supports the assumption that the activations underlay different processes for go and no-go trials.

Recent neuroimaging work suggests that conflict resolution primarily – or even exclusively – works through amplification of task-relevant information, rather than inhibiting task-irrelevant processing (Egner and Hirsch, 2005). Accordingly, we expected to find indication for enhanced color processing, in terms of increased activation in color processing visual cortices, particularly the lingual gyrus, in response to incompatible effect tones assumed to induce conflict between incompatible response tendencies. This expectation was not confirmed which we attribute to the fact that behavioral conflict during response execution (after response selection) was too weak to evoke amplificatory control processes (see above). Instead, we found increased activation in the lingual gyrus in response to effect tones presented during no-go trials. No-go trials that include effect tones can be reasonably considered a conflict condition as well, with conflict occurring between the execution and the withholding of the tone-associated response. Thus, lingual gyrus activation during no-go trials may likewise reflect control efforts to enhance task-relevant color processing in order to ensure task-appropriate performance.

Summary and conclusion

In the present study, we identified neural activations that underlie ideomotor processes, particularly effector activation and facilitation/interference effects by the perception of learned action effects. We could thus replicate and extend results of Elsner et al.'s (2002) previous study. In more detail, evidence for direct effector activation by the passive perception of learned action effects was provided by activation in a number of motor-related brain regions (SMA, premotor cortex, somatosensory cortex, and cerebellum). Importantly, this effect was exclusively present for left-hand action effects whereas activations related to right-hand action effects did not substantially differ from brain activations related to otherwise comparable auditory stimuli. The latter finding is suggestive of a basic modulation of ideomotor learning by response laterality and/or the agent's handedness which, however, is speculative and needs further investigation. Moreover, brain activations in response to action effects during the pursuit of goal-directed action – which essentially comprised the posterior prefrontal and temporo-parietal cortex – suggest that action effects attracted special attention and thereby engaged selective cognitive control processes to ensure task-appropriate performance. Furthermore, response-incompatible compared to response-compatible effect tones elicited stronger activation in the premotor cortex and SMA which can be reasonably interpreted as reflecting differential requirements on the motor system. Even though not reflected in the present behavioral data, differential premotor involvement may underlie interference or facilitation effects as they were repeatedly found in behavioral studies.

Acknowledgments

This research was supported by a grant of the German Research Foundation (Deutsche Forschungsgemeinschaft; DFG) to O.G. and B.H. (GR 1950/1-3 and HO 1430/8-1; Priority Program 1107 “Executive Functions”).

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