Linking Actions and Their Perceivable Consequences in the Human Brain

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Voluntary action is goal-directed and therefore depends on the ability to learn associations between movements and their perceivable consequences. The neural substrate of this ability was investigated with $H_2{}^{15}O$ positron emission tomography (PET). Healthy adults first learned that self-initiated keypresses were consistently followed by certain tones (i.e., action effects). During PET imaging, participants listened to varied ratios of action–effect tones and neutral tones without performing any movement. The caudal supplementary motor area and the right hippocampus increased their activity with the frequency of action–effect tones, suggesting that both cortical areas play a role in linking the consequences of an action and the action itself. This integration process represents a highly flexible mechanism that helps to promote the learning, automatization, and control of voluntary actions. © 2002 Elsevier Science (USA)

INTRODUCTION

During the past decades, understanding the neural mechanisms of voluntary action has been one of the key issues in neuroscience. A great deal of research in this field has focused on the acquisition of arbitrary sensorimotor associations, that is, associations between sensory cues and subsequent actions that lack any systematic relationship (Kurata *et al.,* 2000; Sakai *et al.,* 1999; Toni and Passingham, 1999; Wise and Murray, 2000). However, the key feature of voluntary action is that these actions are commonly not prompted by sensory cues, but rather guided by intentions: The agent intends to achieve a certain goal or to produce a desired effect (Prinz, 1997). For example, musicians play the piano not because seeing the keyboard trig-gers keypressing movements, but because they wish to produce a particular melody.

To perform an intentional action, the agent needs to know what consequences a particular movement will have. Hence, voluntary action depends on the ability to learn associations between movements and their perceivable consequences. According to the well-known ideomotor principle put forward by William James (1890) and others in the 19th century, performing a movement and perceiving a sensory event in close temporal succession lead to the integration of the corresponding motor and perceptual codes. Like sensorimotor mapping, ideomotor learning consists in acquiring a consistent relationship between a motor event and a sensory event, and it is likely that both types of learning rely on associative learning mechanisms integrating events that frequently occur in close temporal succession. However, ideomotor and sensorimotor learning tap different aspects of the learning situation. By sensorimotor mapping, people learn associations between cueing stimuli and subsequent actions, whereas by ideomotor learning, they acquire associations between actions and subsequent sensory events (i.e., perceived action effects). Thus, when playing the piano, both types of learning may be present, but sensorimotor mapping would associate the finger movement to the sight of the note, whereas ideomotor learning would associate the finger movement to the hearing of the tone. Moreover, the two types of learning serve different behavioral functions: While sensorimotor mapping helps to adapt behavior to the environment (Kurata *et al.,* 2000), ideomotor learning helps to adapt behavior to the agent's intentions. Indeed, without learning associations between actions and their consequences, agents are unable to plan a movement that is appropriate to achieve a desired action goal.

The ideomotor principle claims that intentional actions can be triggered by anticipating their consequences (Hommel *et al.,* 2002; Prinz, 1997). Thus, per-

ceiving or imagining the perceptual effects of an action should activate those brain areas that plan and execute this action. Consistent with this expectation, behavioral studies indicate that perceiving a learned action effect facilitates the movement that had previously caused this effect (Elsner and Hommel, 2001; Hommel, 1996). In these studies, participants first worked through a learning phase, in which self-produced keypresses were followed by certain tones. In a subsequent test phase, participants performed the same kinds of keypresses, but now the tones were presented as imperative stimuli to signal the responses. In this test phase, the response that previously had produced the present stimulus tone (i.e., the acquisition–consistent response) was performed faster than the response that had produced the alternative tone (i.e., the acquisition–inconsistent response). Thus, the results indicate that the perception of a learned action effect resulted in a "backward" activation of the associated movement: The participants had learned associations between the keypresses and the subsequent tones in the learning phase and these associations mediated response activation in the test phase.

Whereas recent work has identified much of the neural network that underlies arbitrary sensorimotor mapping (see Wise and Murray, 2000, for review), the neural basis of ideomotor learning is still unknown. We employed $H_2{}^{15}O$ positron emission tomography (PET) to delineate the neural structures linking the perceivable consequences of an action to the action itself. In the present experiment, healthy adults first learned that self-initiated keypresses (i.e., actions) were consistently followed by certain tones (i.e., action effects; Fig. 1A). During PET imaging, participants listened to action–effect tones and neutral tones without performing any movement (Fig. 1B). Employing a parametric design, we varied the ratio of action–effect to neutral tones across scans (Fig. 1C) and mapped cortical regions that gradually changed their neural activity depending on the relative frequency of perceived action–effect tones.

The design of study differs from previous functional imaging studies on arbitrary sensorimotor mapping (Grafton *et al.,* 1998; Kurata *et al.,* 2000; Toni and Passingham, 1999; Weeks *et al.,* 2001) in essential aspects: First, subjects experienced a consistent relation between a movement (i.e., action) and a following sensory event (i.e., learned action effect), but not between a cueing sensory event and a following movement. Second, the association between the action and the effect is to be learned "incidentally," not by instruction or reinforcement. Third, cerebral activity was recorded after considerable learning and in the absence of any movement, thereby looking for a "backward" activation of the learned association.

Following up on the behavioral studies, the main aim of this study was to examine whether the mere perception of a learned action effect is sufficient to activate cortical areas that are known to be involved in manual motor control, such as the lateral premotor cortex and the supplementory motor area (SMA). In addition, we were interested in defining those brain areas that are specifically involved in the retrieval of learned action–effect associations. If parts of the neural network underlying arbitrary sensorimotor mapping (i.e., dorsal premotor cortex, hippocampal system, basal ganglia, and cerebellum; cf. Wise and Murray, 2000) would also be activated by the perception of learned action effects, this would point to a rather general role for these structures in learning associations between sensory and motor events.

MATERIALS AND METHODS

Subjects

Eight healthy right-handed male subjects (ages 27–39 years; mean age 30.8 years) participated in the study. Informed consent was obtained prior to participation. The study was approved by the local ethics committee.

Experimental Design

The participants were scanned in supine position with their eyes closed, their index fingers resting on 3-mm keys with a horizontal distance of 30 cm. The keys were mounted on a 50 × 40-cm board that rested on the participant's abdomen. The board as well as the participant's shoulders and arms was supported by foam blocks.

Prior to the first PET scan, the participants performed 200 learning trials. In each trial, a beep (50-ms 1570-Hz sinusoidal tone) signaled to press a key with the left or right index finger. Participants were instructed to press the keys in a random sequence and about equally often over the learning trials. After each keypress, a certain MIDI tone was presented for 200 ms through in-ear headphones: a 392-Hz organ tone, a 587-Hz sinusoidal tone, or a 784-Hz trumpet tone. The assignment of tones to keys and the neutral tone used during scans was balanced across participants. To foster incidental learning, the subjects were instructed to roughly balance the frequencies of the two responses across the trials; the tones, they were told, would be not important for the task but would only indicate the registration of the keypress. Further blocks of 60 learning trials were administered after the 2nd, 5th, 7th, and 10th PET scan.

Each participant underwent 12 PET scans. During each scan, two different tones were presented in a random sequence: a 200-ms action–effect tone (i.e., in 6 PET scans, the tone that had followed the left keypress; in the other 6 PET scans, the tone that had followed the right keypress) and a 200-ms neutral tone
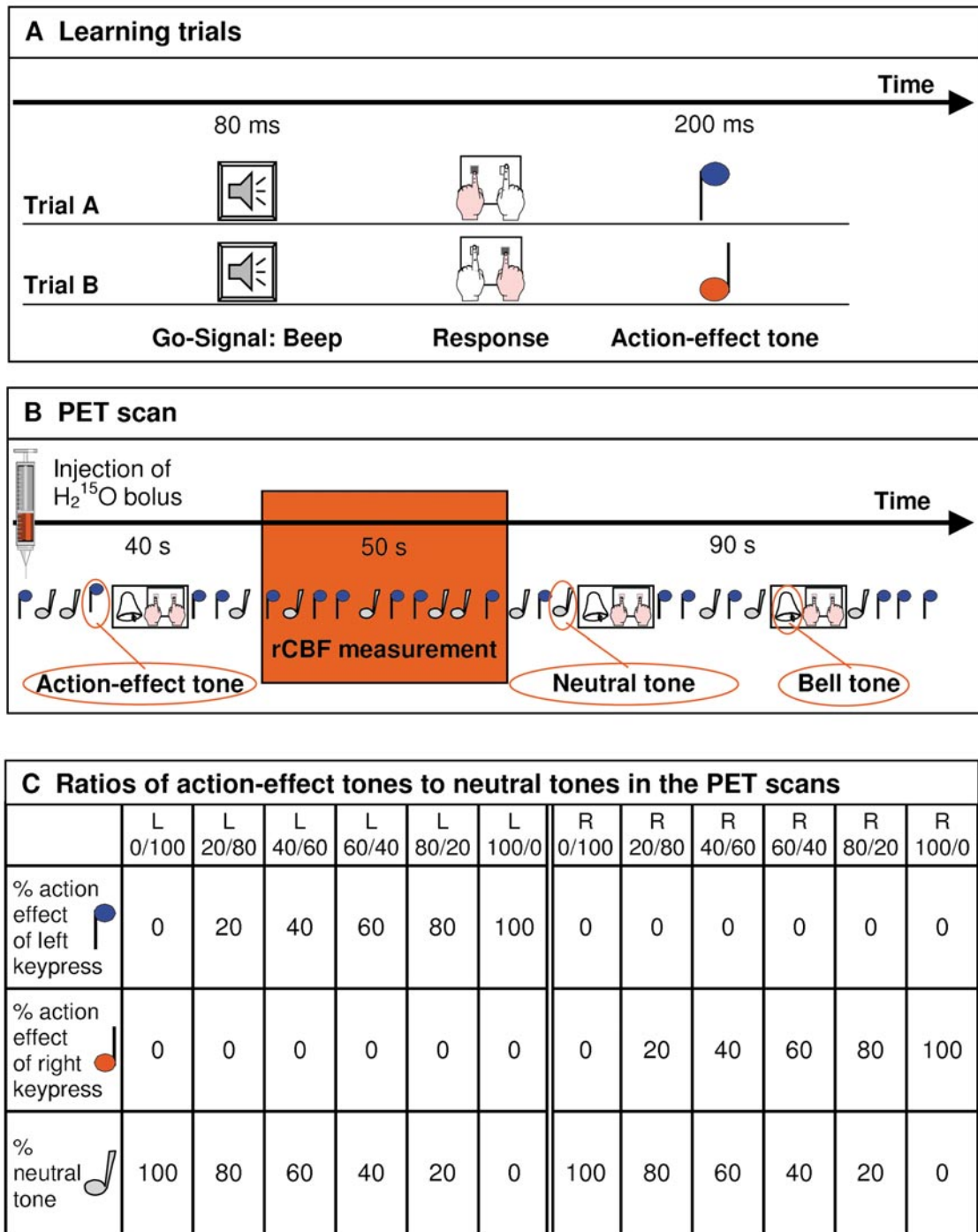
FIG. 1. Experimental design of the learning trials and of the PET scans. (A) Learning trials. 200 learning trials were conducted prior the first PET scan. Subjects were instructed to press a key with the left or right index finger after a short beep signal. Over the learning trials, the keys were to be used in a random sequence and about equally often. After each keypress, a certain tone (i.e., action effect) was presented. Further blocks of 60 learning trials were conducted after the 2nd, 5th, 7th, and 10th PET scan. (B) PET scan. During each PET scan, an action–effect tone (i.e., previously related to a keypress) and a neutral tone (i.e., not related to a keypress) were presented in a random sequence. The participants' task was to merely listen to the tones. To maintain attention, participants were required to press both keys simultaneously whenever a short bell tone appeared. As this tone never appeared during the 50-s period of rCBF measurement, the analyzed brain activity reflects listening to the action–effect and neutral tones without performing any movement. (C) Ratios of action–effect tones to neutral tones in the PET scans. The action–effect tone and the neutral tone were presented in a different ratio in each of the 12 PET scans. There were six ratio conditions (0/100, 20/80, 40/60, 60/40, 80/20, 100/0) for the action effect of both the left (L) and the right keypress (R). The succession of the ratios over the 12 scans was counterbalanced across participants.
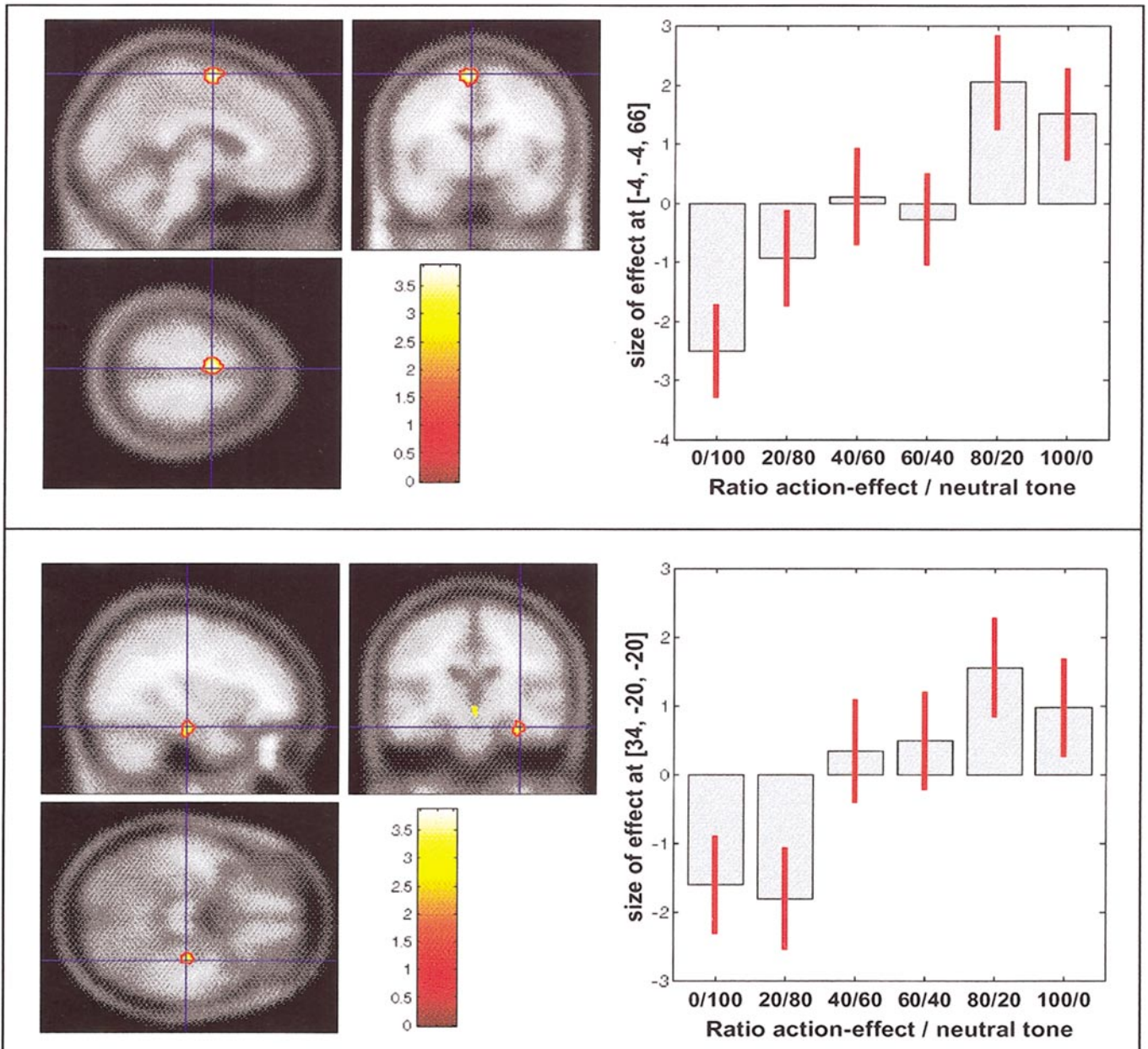
FIG. 2. Foci in the supplementary motor area and the right hippocampus showing a linear relationship between functional activation (as indexed by rCBF) and the proportion of perceived action–effect tones per PET scan ($p < 0.001$). The yellow area illustrates the extent of activation in the sagittal, coronal, and horizontal plane according to the MNI stereotaxic space. The bar charts represent parameter estimates for the average activations (±standard error) in the peak voxels depending on the ratio of perceived action–effect tones per PET scan in all eight participants. For illustrative purposes, the ratios are displayed in a fixed order, so that the proportion of perceived action–effect tones increases from left to right. (Top) Activation in the supplementary motor area. Talairach coordinates of peak ($Z = 3.68$) activity: $x = -4$, $y = -4$, $z = 64$. (Bottom) Activation in the right posterior hippocampus. Talairach coordinates of peak ($Z = 3.36$) activity: $x = 34$, $y = -20$, $z = -20$.

(i.e., not related to a keypress). The intertone interval varied randomly between 800, 1000, and 1200 ms. Background noise and average frequency of presented tones were constant throughout. In each scan, the ratio of action–effect tones to neutral tones was set to one of the following conditions: 0/100, 20/80, 40/60, 60/40, 80/20, or 100/0. Sequences with "left" and "right" ac-

tion–effect tones alternated over the 12 scans, and the succession of the ratios was balanced across participants. The tone presentation started 40 s before and ended 90 s after each 50-s period of the regional cerebral blood flow (rCBF) measurement.

During the 12 PET scans, the participants' task was to listen to the neutral and action effect tones without

pressing any key. However, to ensure a comparable level of attention among scans, participants were additionally instructed to press both keys simultaneously whenever they heard a short bell tone (80-ms 1570-Hz marimba) (cf. Stephen *et al.,* 1995). Because we sought to investigate the perception of learned action effects in absence of any movement, the bell tones were presented only during the 40 s before and the 90 s after, but never during rCBF measurement. The bell tones sounded irregularly, with one tone presented in a 20-s interval, so participants did not notice the absence during the 50-s rCBF period. On average, participants heard 25 tones and 2 bell chimes before, 35 tones during, and 65 tones and 4.5 bell chimes after rCBF measurement. To control for covert finger movements, continuous surface EMG recordings were obtained from both first dorsal interosseus muscles (band-pass filtering 10 to 1000 Hz). Moreover, eye movements were assessed by surface electrodes placed bilaterally over the zygomatic region (band-pass filtering 0.1 to 10 Hz).

PET Data Acquisition, Image Processing, and Statistical Analysis

PET scans were obtained using a Siemens ECAT EXACT HR+ (Model 962) PET scanner (CTI, Inc., Knoxville, TN). Scanning was performed in three-dimensional mode with a total axial view of 15.5 cm and no interplane dead space, allowing for the whole brain to be imaged. Participants received 12 intravenous boluses (250 Bq) of radioactively labeled water ($H_2^{15}O$) infused over 20 s followed by a 20-s saline flush through a forearm canula, each bolus administered about 10 min apart. A 20-min headholder transmission scan with a rotating 68Ge/68Ga source was obtained prior to the first rCBF measurement in order to correct for effects of radiation attenuation.

Images were reconstructed into 128 by 128 pixels in 63 planes with an in-plane resolution of 6.5 mm and were analyzed with SPM'99 (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl. ac.uk). To correct for head movements, all scans were realigned to the first scan. Following realignment, PET images were transformed into stereotactic space using a template from the Montreal Neurological Institute (MNI) and were smoothed using an isotropic Gaussian kernel of 12 mm full width at half-maximum. Each voxel of the resulting images was $2 \times 2 \times 4$ mm in size (Friston *et al.,* 1995; Talairach and Tournoux, 1989). Global variance between conditions was removed by analysis of covariance (ANCOVA). For each voxel, condition-specific adjusted rCBF values with an associated adjusted error variance were generated. Using linear weighted contrasts, we estimated areas showing a linear relationship between the relative frequency of action–effect tones per PET scan and the normalized

rCBF, according to the general linear model and theory of Gaussian fields at each voxel. The generated SPM[*t*] maps were transformed into normally distributed SPM[*Z*] maps. Significance level was set at a *p* value of 0.001 (uncorrected) corresponding to a *Z* score of 3.21.

RESULTS

Behavioral Data

For the five learning phases, *t* tests revealed that the ratio of left and right keypresses did not differ from chance (50/50) in any phase (phase 1, 51/49, $p > 0.10$; phase 2, 48/52, $p > 0.20$; phase 3, 51/49, $p > 0.20$; phase 4, 51/49, $p > 0.20$; phase 5, 50/50, $p > 0.40$). Thus, the subjects experienced both action–effect couplings about equally often. An analysis of variance (ANOVA) revealed that the reaction times were about the same in each of the five learning phases (271, 266, 292, 269, and 303 ms, respectively; $F(4,28) = 0.58$, $p > 0.60$).

During the critical period of rCBF measurement, participants were required to listen to the neutral and action–effect tones without pressing any key. Subjects made no errors in this task at all. Additionally, surface EMG and oculographic recordings revealed that none of the participants performed covert finger or eye movements during rCBF measurements. Thus, the recorded brain activity actually reflects listening to tones without performing any movement.

Before and after the critical rCBF period, bell tones appeared, and participants were required to press both keys simultaneously after each bell tone. Subjects made very few errors: They missed 0.7% of the bell tones (maximal number of misses 2.9% in scan "left 40/60"), and the average number of false alarm responses (i.e., keypresses after a neutral tone or an action effect tone) was 0.2% (maximal number of false alarms 0.5% in scan "left 0/100"). None of these errors occurred during rCBF measurement, and the number of errors was not correlated with the ratio of action–effect tones to neutral tones in the scan.

In a final screening, none of the participants reported motor imagery of any kind (i.e., of keypresses as such or of the keypresses associated with action–effect tones). Moreover, none of the participants had noticed that he participated in a learning study. Although six of the eight subjects realized that each keypress was followed by a certain tone in the learning phase, only one could tell what the tones sounded like. His brain activity was not different from that of the others. Thus, our instruction succeeded in creating incidental learning.

PET Results

Statistical parametric mapping revealed two foci showing a linear positive relationship between func-

tional activation and the relative frequency of perceived action–effect tones per PET scan. The first focus of activation was located in the SMA just posterior to the vertical anterior commissural (VAC) line (peak activity: Z score = 3.68; Talairach coordinates of peak activity in mm, $x = -4$, $y = -4$, $z = 64$; Fig. 2). The VAC line has been proposed as the approximate anatomical landmark separating the functionally different caudal (i.e., SMA proper) and rostral part (i.e., pre-SMA) of the SMA in humans (Deiber *et al.,* 1991; Zilles *et al.,* 1996). Thus, the first focus was located in the rostral SMA proper. The second focus was located in the right medial temporal cortex covering the posterior part of the hippocampus (peak activity: Z score = 3.36; Talairach coordinates of peak activity in mm, $x = 34$, $y = -20$, $z = -20$). No brain area showed a negative linear relationship between rCBF and the frequency of response-related tones per PET scan.

In order to assess effector-specific foci of activation, we computed separate SPM analyses that included only those PET scans during which either "right" or "left" action–effect tones had been presented (i.e., five scans per participant). No focus in the lateral premotor cortex or the SMA showed a linear relationship between the relative frequency of "left" or "right" action–effect tones per PET scan and normalized rCBF. The focus of activation in the right hippocampus reached significance only for action–effect tones associated with the right hand (peak activity: Z score = 3.46; Talairach coordinates of peak activity in mm, $x = 34$, $y = -20$, $z = -26$) and not for action–effect tones associated with the left hand.

DISCUSSION

The key finding of this study is that in healthy human adults, the mere perception of learned action effects results in a circumscribed activation in the rostral SMA proper and in the right posterior hippocampus. Since both the SMA proper and the right hippocampus show a gradual increase in neuronal activity with the proportion of response-related tones per PET scan, neuronal activity in these areas specifically reflects the cortical representation of the previously learned arbitrary association between actions (i.e., keypresses) and action effects (i.e., tones).

SMA Activation by the Perception of Learned Action Effects

The graded increase in functional SMA activation confirmed our hypothesis that the mere perception of a learned action effect is sufficient to activate cortical areas that are involved in manual motor control. The rostral SMA proper is known to be involved in the planning of simple hand movements (Stephan *et al.,* 1995; Tyszka *et al.,* 1994). In the present study, how-

ever, behavioral data and EMG recordings confirmed that participants followed the instruction and did not move their fingers or imagine doing so during rCBF measurement. Thus, we interpret the gradual activation of the rostral SMA proper during perception of action–effect tones as evidence for a backward activation of the associated simple hand movement (i.e., keypress). The fact that this backward activation occurred even though the action–effect tones did not serve as a cue to initiate the movement is in keeping with behavioral data (Elsner and Hommel, 2001) and provides strong evidence for our hypothesis that response activation by the perception of learned action effects is an automatic and obligatory process (Hommel *et al.,* 2002; James, 1890; Prinz, 1997). Hence, the backward activation is reminiscent of automatic activation of motor structures during classical conditioning (Buechel *et al.,* 1998) and quite different from conscious preparation of a self-initiated motor act. This may be the reason why other frontal motor areas that are known to be involved in conscious motor preparation did not show any activation in the present study.

Although some brain imaging studies report that the SMA is active during motor inhibition, several aspects of our study support the notion that the SMA activation was actually due to automatic response activation: First, the focus was located in the SMA proper, whereas response inhibition is consistently located in the pre-SMA (Elliott and Dolan, 1999; Humberstone *et al.,* 1997; Krams *et al.,* 1998; Waldvogel *et al.,* 2000). Second, the anterior cingulate cortex and the ventrolateral prefrontal cortex, which have been consistently shown to be engaged in response inhibition (Braver *et al.,* 2001; Rubia *et al.,* 2001), were not activated in our study. Third, our subjects made only a few errors in the task of listening to the tones and pressing both keys simultaneously when a bell tone appeared, and they made no errors at all during rCBF measurements. If one nevertheless assumes that the SMA activation is connected to the inhibition of the double keypress, this activation should be about the same in all 12 scans, because they consisted of the same amount of "Go" (i.e., bell tones) and "NoGo" signals (i.e., action–effect and neutral tones). Indeed, the positive correlation between SMA activity and the frequency of perceived action–effect tones provides the strongest argument for automatic response activation: Even if this SMA activity would reflect the inhibition of the left or right single keypress, the correlation would indicate that the more action–effect tones are perceived, the more motor inhibition is needed. Thus, if the SMA activation did reflect motor inhibition, then it would be only to counteract the backward response activation caused by the perception of action effects.

The present data are in accordance with current knowledge about the functional differentiation of the SMA with regard to learning and automatization of

movements: Previous functional imaging studies on the acquisition of arbitrary visuomotor associations or motor sequences have shown that the pre-SMA is particularly active at early stages of learning, whereas activity in the SMA proper increases as learning progresses (Jenkins *et al.,* 1994; Sakai *et al.,* 1999; Toni *et al.,* 1997; Toni and Passingham, 1999). As associations between keypresses and tones were highly overlearned at the time of PET scanning, our findings support the notion that the SMA proper is a critical structure for the automatization of behavior. Moreover, our data extend previous studies on arbitrary auditorimotor mapping (Kurata *et al.,* 2000; Weeks *et al.,* 2001) by showing that the SMA is capable not only of linking movements to preceding auditory stimuli, but also of linking movements to their subsequent auditory consequences. The associations between the actions and their consequences were learned incidentally without any reinforcing instruction. Hence, close temporal succession is sufficient for establishing ideomotor associations, and the SMA seems to be a key motor structure for this automatic associative learning (Hazeltine *et al.,* 1997).

The lack of effector-specific activations in the second set of analysis suggests that the learned association remained at an abstract level and, thus, the action effect was not specifically linked to the motor effector (i.e., the right or left hand). However, there are two reasons we hesitate to draw strong conclusions from this observation. First, behavioral evidence does suggest that the perception of action effects may well reach the effector level if it prompts the execution of the associated action (Elsner and Hommel, 2001). Hence, the lack of effector-specific activations may be due to the fact that our subjects were not required to carry out the actions signaled by the effect tones. Second, it is important to keep in mind that the statistical power of effector-specific analyses was much lower than that of the overall analysis, since only 5 of the 12 scans were included. Therefore, the absence of effector-specific effects should be treated with caution until it can be replicated with greater statistical power and under conditions under which subjects are allowed to react on the learned action–effect tones.

The activation of the rostral SMA proper during the perception of learned action–effect tones further corroborates the idea that there is no rigid dichotomy between internally and externally guided motor behavior (Deiber *et al.,* 1999; Grafton, 1994; Tanji and Shima, 1994). In accordance with the ideomotor principle (Hommel *et al.,* 2002; Prinz, 1997), the present findings suggest that a self-initiated movement that is consistently followed by a certain sensory event becomes to some degree externally guided by this learned action effect. The capability of the SMA to store abstract representations of actions and their perceivable consequences provides a neuronal substrate for a flexible adaptation of self-initiated motor behavior depending on the intended action goals.

Activation of the Hippocampus

The second focus showing a gradual increase in rCBF with the frequency of response-related tones was located in the right posterior hippocampus. Recent functional imaging work has confirmed that the hippocampal system is critically involved in relational or associative memory processing (Henke *et al.,* 1997; Wise and Murray, 1999). The gradual increase in hippocampal activation during the perception of action–effect tones most likely reflects the retrieval of the learned associations. The right-hemispheric hippocampal activation corresponds to studies suggesting that the right hippocampus is preferentially involved in memorizing sounds (Cohen *et al.,* 1999).

Our findings stress two characteristic features of hippocampal memory binding. First, relational memory processing in the hippocampus is not limited to complex stimuli such as words, faces, or scenes. In the present study, subjects learned associations defined by the close temporal succession of simple motor events (i.e., keypresses) and following simple sensory events (i.e., arbitrary tones), and thus, our findings support the notion that the hippocampus is involved in simple procedural, or habit-based, learning tasks (Gluck *et al.,* 1997). Second, subjects learned the association between the keypresses and the action–effect tones incidentally without any reinforcing instruction. Moreover, the retrieval of the learned action–effect association, which occurred during PET scanning, was not reinforced by the instruction. By contrast, the given instruction served as a distracter with regard to the neural effect of interest (i.e., perception of varying frequencies of learned action–effect tones) by shifting the participant's attention toward the bell tone. Accordingly, our study provides support for the idea that relational memory binding in the hippocampus is an automatic and obligatory process (Cohen *et al.,* 1999).

Methodological Considerations

Our finding that the rostral SMA proper and the posterior hippocampus were the only foci activated by the perception of learned action effects does not mean that these are the only brain areas engaged in ideomotor learning. Since our participants were imaged at the end stage of learning, the data do not provide any information about areas that are engaged in *encoding* associations between actions and their perceivable consequences, but only about areas that are engaged in *retrieving* these associations. Moreover, we adopted a parametric study design, which has been shown to provide a powerful approach to pinpoint a specific set of brain areas being involved in a distinct cognitive process (Boecker *et al.,* 1998; Turner *et al.,* 1998). How-

ever, compared to a categorical comparison between two tasks, a parametric approach is less suitable for demonstrating all brain regions that are involved in a given cognitive process.

Thus, the results of the present study do not justify the claim that learned associations between actions and their perceivable consequences are exclusively represented in the two indicated brain regions. On the contrary, other brain areas, like the dorsal premotor cortex, the basal ganglia, and the cerebellum, may be active in a different experimental context, like when subjects are imaged during the acquisition of action–effect associations or when subjects are actually required to carry out finger movements after the perception of learned action–effect tones. Moreover, since the dorsal premotor cortex is crucial for visuomotor mapping (Grafton *et al.,* 1998; Murray *et al.,* 2000), it is conceivable that this area may also be engaged in the learning of associations between actions and their visual consequences.

CONCLUSION

The key finding of this study was that the mere perception of learned action effects resulted in a circumscribed activation of the rostral SMA proper and of the right posterior hippocampus. As both brain areas show a gradual increase in neural activity with the perceived frequency of action–effect tones per PET scan, they seem to be engaged in the cortical representation of the learned association between keypresses (or actions) and tones (or action effects). To the best of our knowledge this is the first study demonstrating a distinct set of cortical areas that are engaged in the retrieval of learned associations between self-initiated actions and their perceivable consequences—even though the methodological constraints of the study design do not allow one to conclude that the SMA and the hippocampus are the only brain regions involved in action–effect learning. Since the backward activation of an action by the perception of its learned action effects is of behavioral relevance for motor performance (Elsner and Hommel, 2001; Hommel, 1996), our findings confirm the crucial role of the SMA and the hippocampus in the guidance of goal-directed, voluntary actions.

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