Dissociating Networks of Imitation

Mareike M. Menz,^{1,2} Adam McNamara,^{1,2} Jane Klemen,^{1,2}
and Ferdinand Binkofski^{1,2*}

¹Department of Neurology and Neurolmage Nord, University Hospital Schleswig-Holstein,
Campus Luebeck, Germany

²Department of Systems Neuroscience and Neurolmage Nord, University Medical Center
Hamburg-Eppendorf, Hamburg, Germany

Abstract: The investigation of imitation, which consists of observation and later reproduction of voluntary actions, promises insights into the complex processes of human actions. Although several aspects concerning the component neural processes necessary for action execution are known, our current understanding of the neural networks underlying these remains sparse. The present study applies independent component analysis (ICA) to functional magnetic resonance imaging (fMRI) data acquired during imitation of abstract gestures and object-related actions. This enables identification of neural networks underlying the production of these imitations. The explorative approach of ICA is complemented by an analysis of time courses from the maxima of each component. Four independent networks were active during delayed imitation. These can be assigned to the aspects of (1) action perception, (2) motor preparation and action execution, (3) encoding and retrieval into and from working memory, as well as (4) the dynamic integration of object affordances into the action. At least two of these networks participate in action preparation, one contains areas involved with motor working memory and one includes areas which are connected to the true action execution. The fourth network only shows activity shortly before an object-related action is imitated. This indicates a late integration of object affordances into the movement as the time course of activity in this network pertains to action rather than perception of the object. *Hum Brain Mapp* 30:3339–3350, 2009. © 2009 Wiley-Liss, Inc.

Key words: action preparation; affordances; imitation; independent component analysis; motor working memory; observation

INTRODUCTION

Since Hugo Liepmann's research on apraxia at the beginning of the 20th century, the question as to how cognition and motor control interact remains a crucial topic for neuroscientific research. One main approach to this issue is to identify the steps which have to be taken from perception to action. A commonly used method to trigger a voluntary execution of an action is imitation. Delayed imitation has been employed to disambiguate motor working memory from sensory and motor aspects of action execution (Leung et al., 2002). Apart from the intention to move there are several aspects that cause activation in a delayed imitation task. The first aspect is the perception during the presentation of an action, which is to be imitated, while the second is the encoding of this content into working

Contract grant sponsors: Volkswagenstiftung (I/79006) (to A.M. and F.B.), NeuroImage Nord, BMBF (01GW0571) (to M.M.M. und F.B.), and EU-FP7-ICT-2007-1.

*Correspondence to: Ferdinand Binkofski, Department of Neurology and Neurolmage Nord, University of Luebeck, Ratzeburger Allee 160, D-23538 Luebeck, Germany.

E-mail: ferdinand.binkofski@neuro.uni-luebeck.de

Received for publication 1 September 2009; Revised 20 January 2009; Accepted 21 January 2009

DOI: 10.1002/hbm.20756

Published online 2 April 2009 in Wiley InterScience (www.interscience.wiley.com).

memory. The third aspect can be described as the pure maintenance in working memory, the fourth being retrieval from working memory. The fifth aspect is the action preparation and the final aspect is the actual execution of the movement. These aspects might overlap in time as well as they might rely on overlapping neuroanatomic structures. An area important to more than one aspect may also be accessible via different pathways. This diversity of aspects within the imitation task is also reflected by the areas reported for imitation. The frontoparietal mirror neuron circuit plays an important role in imitation. It consists of the inferior parietal lobe, the premotor cortex and the inferior frontal gyrus (Buccino et al., 2004), especially BA44/45 (Iacoboni et al., 1999; Makuuchi, 2005), additionally working memory areas are reported such as the lateral prefrontal cortex (D'Esposito et al., 1999) and the supplementary motor area (SMA) (Petit et al., 1998). Imitation constitutes a complete perception-to-action process, consequently action and perception areas of the two visual pathways (Goodale and Milner, 1992) as well as motor areas like the primary motor cortex (M1), the premotor cortex (PMC) and the SMA seem to be important. If the movement also contains an object, the anterior inferior parietal sulcus has been reported to be active for grasping as has the inferior parietal lobe and the middle frontal gyrus when the subject was asked to manipulate the object (Binkofski et al., 1999; Johnson and Grafton, 2003). Furthermore, the superior parietal lobe, the superior temporal sulcus and the posterior cingulate gyrus were reported to be active during the integration of object properties (Binkofski et al., 1999; Grezes et al., 2003; Mecklinger et al., 2002).

Several subdivisions between the different aspects of preparation and execution of imitated actions have been investigated previously. Different activation patterns were reported for maintenance and execution (Koch et al., 2005; Makuuchi, 2005; Toni et al., 2002; Volle et al., 2005), motor preparation and motor execution (Krams et al., 1998; Petit et al., 1998; Thoenissen et al., 2002), and also for storage and processing components in working memory (D'Esposito et al., 1999; Leung et al., 2002, 2007). Although Habeck et al. (2005) applied principal component analysis to data from a delayed-match-to-sample task in order to distinguish among stimulus, retention and probe of working memory content, findings concerning the networks underlying those aspects of object- and non-object-related actions require further investigation.

In neuroimaging, the identification of real networks as opposed to synchronous activation patterns remains difficult. Common activation patterns, as revealed by linear contrasts between conditions, do not necessarily link to the same network. Independent component analysis (ICA) is one robust method for analyzing common sources of variance for independent networks. In functional magnetic resonance imaging (fMRI) it is used to identify sets of statistically independent spatial maps, together with their associated time courses (Comon, 1994; Beckmann and Smith, 2004). This means a set of statistically independent networks is detected. As the

areas within a network share a common time course an independent component displays all areas which are active at the same time. This is an advantage over the contrast-based evaluation, which displays areas of difference within a presumptively existing network.

The aim of our study was to find different independent components for perception and execution of object- and non-object-related actions and to distinguish different networks active during the delay period. Apart from the identification of independent networks, we wanted to investigate the similarities and differences of object-related actions and abstract gestures, as it appears to be important whether movements contain objects, either real or imagined, as in pantomime, or are simply defined by abstract gestures. Comparisons between object-related movements and abstract gestures suggest different activation patterns for these movement types (Binkofski et al., 1999; Buccino et al., 2001). The role of the object within movements is embedded in several theoretical frameworks. The goal directed theory of imitation suggests physical things, i.e. objects as goals, to drive human imitation (Bekkering and Wohlschläger, 2002). This presence of a goal is also reported to increase activation in areas relevant to motor preparation and execution (Koski et al., 2002). This goal directed theory of imitation also uses the concepts of goals at another more functional level, as described by the ideomotor principle of Greenwald (1970), which states that the selected physical goals elicit the motor program with which they are most strongly associated. This essential influence of the object on a motor action is also substantial to the theory of affordances. First introduced by Gibson (1977), affordance is a quality of an object, or an environment, that allows an individual to perform an action in, on, or with it. Indeed there is evidence for a perception-based processing of affordances directly caused by the object (Ellis and Tucker, 2000), which is also directly eliciting motor programs. On the other hand, it has been suggested that the integration of affordances is connected to the possibility to act rather than to pure perception (Tipper et al., 2006). Therefore the integration of object affordances into the perception-to-action process could possibly occur during perception, during action or in between, e.g. during action preparation.

We hypothesized that the different aspects of imitation are grounded in different neural networks. Moreover we hypothesized that object-related actions contain more aspects of dynamic processing than abstract gestures. These include the implementation of spatial coordinates of the object, as well as the integration of object affordances into the movement (Gibson, 1977). This should be reflected in either higher activation or in an extra network component including some or all of the object sensitive areas described above.

MATERIALS AND METHODS

Subjects

Fifteen healthy right-handed volunteers (eight females, mean age 27.5 years) underwent successful data

acquisition. Each subject gave written informed consent and the study was approved by the local (Hamburg Board of Physicians) ethics committee.

Delayed Imitation Task

During the construction of our task we opted, on the one hand, for the most natural conditions possible: although an egocentric perspective bears advantages as compared with allocentric perspective, e.g. is connected to a better visual and kinaesthetic imagery and needs less mental rotation (Jackson et al., 2006), stimuli were presented in the third person perspective as this is the natural condition for imitation. However, all videos were presented from a specular viewpoint, as if watched in a mirror, since developmental studies indicate that specular imitation is a more natural behavior than anatomic imitation (Bekkering et al., 2000). It is also likely to elicit higher responses than an anatomical viewpoint (Koski et al., 2003).

Subjects were allowed to see their hands and the objects throughout the full imitation movement to allow for an accurate movement (Churchill et al., 2000). For the same reason all trials were movement imitations instead of posture imitations and the object-related actions included real object interactions. On the other hand, the task allowed controlling for a possible difference between object- and non-object-related actions, in that we implemented object-related actions as well as abstract gestures (Binkofski et al., 1999; Buccino et al., 2001). Since there is evidence that meaningful gestures are encoded differentially (Decety et al., 1997) and that long-term memory can be used for imitation (Rumiati and Tessari, 2002) we used only novel stimuli as recommended by Buccino et al. (2001, 2004).

To limit anticipatory activity (Toni et al., 2002) the delay period duration was varied in a large range containing 30 different duration periods. With regard to the reduction of movement artifacts, the task employed in this study also contained nonimitation trials, but whether a current trial was to be imitated or not, was unknown to the subject up to the end of the delay period. Additionally, no “no-go” signal was given; instead the next trial followed without interim.

Stimuli

Two sets of video clips were created; one containing abstract gestures, and the other one containing object-related actions. Objects were chosen according to the first six of Biederman’s geons (Biederman, 1987). Geons or geometric icons are designed as simple three-dimensional forms which can be combined into a large possible number of shapes. They are meant to represent all common object form components. To take into account the variety of possible materials and colors, objects were created from several materials. The set contained a brown wooden ring,

a blue hard plastic vertex, a red rubber sphere, a transparent Plexiglas cone, and a green cellular rubber cube.

Every object was combined with several different object-related actions, such as lifting, pinching, rotating, or rolling. In a pilot study 24 of these object-related actions and 26 abstract gestures were presented to 10 subjects, who were asked to imitate them and to rate the difficulty of imitation. In order to include only new movements into the task, the subjects were also asked to name associations to the presented trial. A stimulus was excluded as soon as subjects named a common association to this specific movement. This ensured that only new movements were included in the task. From the initial set of stimuli 20 object-related actions and 20 abstract gestures were chosen. The two subsets differed neither in difficulty (Wilcoxon signed rank test, $P > 0.05$) nor did they bear any common association. All video clips were cut into single frames, to ensure timing of presentation during the experiment. Single frames were presented at a rate of 40 frames/second. Each video displayed hand and forearm, as well as one object in the condition of object-related actions. Examples of stimuli are presented in Figure 1.

Paradigm

The experiment was conceptualised as a $2 \times 2 \times 1$ factorial design, with two experimental conditions “abstract gesture” and “object-related movement,” two modeling conditions “imitation” and “observation” and the parametric factor “delay.” Each trial started with the presentation of a fixation cross for 300 ms, which was followed by the presentation of a video clip (mean duration 2,570 ms, SD = 380 ms, no difference between conditions). After the presentation of the video clip there was a variable delay period of 267–8,010 ms (in steps of 267 ms). At the end of the delay subjects were asked either to imitate the observed movement, which was indicated by a red exclamation mark, or the fixation cross of the next trial appeared on the screen. The observation trials were included to reduce overall task-related motion to 50%, due to less motion artifacts during the perception of videos and the delay period of the following trial. The 20 object-related actions and the 20 abstract gestures were presented three times and imitated or only observed at least once, counterbalanced across trials and subjects. Fifteen null events, during which only a fixation cross was presented, were added to the number of 2×60 stimuli. A restricted randomization ensured an equal distribution of the delay periods, with each delay step once per condition in the first and the second half of the experiment.

Photoelectric barriers were used to ensure that subjects awaited the end of the delay period before starting the imitation movement. Two independent raters scored the correct imitation of movements during the fMRI experiment. Timing of stimuli and temporal logging of light barrier pass in relation to data acquisition were controlled

Figure 1.

Example stimuli of object-related actions (above) and abstract gestures (below). Images are reference frames from the videos.

from a separate PC using “Presentation” (<http://neurobehaviouralsystems.com>). Before scanning, the experiment was explained to the subjects and the correct imitation as well as keeping to the delay periods was practiced until subjects reported being sufficiently familiar with the procedure. Practice trials were not included in the actual experiment. The experiment contained 135 trials, which summed up to a duration of 27 minutes.

fMRI Settings

Subjects lay supine in the fMRI scanner with their head tilted forward (30°). Stimuli were front-projected using a LCD-projector (Sharp PG A20-X) and a custom made translucent screen of 60 × 60 cm at a distance of 370 cm. All six objects were laid out on a table (60 × 12 cm), which was adjusted to each subjects’ comfortable reaching distance (approximately 80 cm from eyes to table) to ensure

uncomplicated object handling. The table was installed so, that all objects lay at about the same distance from the subjects' shoulder joint, so as to avoid movements of shoulder and upper arm. The arrangement of objects on the table was changed from subject to subject. Cushions were positioned beneath the upper arm in order to fix it and restrict any lifting movements. Subjects were instructed to move as little as possible, using mostly their right forearm and hand, while keeping the upper arm and shoulder relaxed and stable.

Image Acquisition

The experiment was carried out on a 3T scanner with an eight-channel head coil (Siemens TRIO, Erlangen, Germany). Thirty-six transversal slices (192 mm FOV, 64×64 matrix, 3 mm thickness, 18% spacing), covering the whole brain were acquired using a fast gradient echo EPI-sequence (TR 2,000 ms, TE 25 ms, 70° flip angle). One functional run with 805 T2* scans was performed, with each scan sampling over the 36 slices. Before the functional run, an anatomical T1-image (256 mm FOV, 256×256 matrix, 1 mm thickness, 20% spacing, TR 15 ms, TE 4.92 ms), was acquired applying a FLASH sequence.

Image Analysis

Data analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.63, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Functional data were motion-corrected using MCFLIRT (Jenkinson et al., 2002). To correct for the temporal offset between the slices acquired in one scan, a Fourier-space time-series phase-shifting was applied. Non-brain voxels were removed using BET (Smith, 2002). To correct for large drifts, a temporal high-pass filter (Gaussian-weighted least-squares straight line fitting) with a cut-off frequency of 1/54 Hz was used for baseline correction of the signal. Spatial smoothing using a Gaussian kernel of FWHM 5.3 mm as well as mean-based intensity normalization of all volumes by the same factor was applied to the functional data. To align the individual functional data slices onto the corresponding 3D stereotactic coordinate reference system (MNI), a rigid linear registration with six degrees of freedom (three rotational, three translational) was carried out using FLIRT (Jenkinson and Smith, 2001).

Statistical Analysis

The first five volumes of each subject's scan were removed to allow for full T1 saturation. All trials rated as "incorrectly imitated" by at least one of the independent raters were excluded from further analysis. A single-session independent component analysis was carried out using MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components) Version 1n(11),

part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl), an implementation for the estimation of a Probabilistic Independent Component Analysis model (Beckmann and Smith, 2004). The following melodic preprocessing was applied to the input data file: masking of non-brain voxels, voxel-wise demeaning of the data, normalization of the voxel-wise variance, whitening and projection into a 25-dimensional subspace of preprocessed data using Principal Component Analysis. The whitened observations were decomposed into a set of time courses and spatial maps by optimizing for non-Gaussian spatial source distributions using a fixed-point iteration technique (Hyvarinen, 1999).

Estimated component maps were divided by the standard deviation of the residual noise and thresholded by fitting a mixture model to the histogram of intensity values (Beckmann and Smith, 2004).

For group analysis only relevant components had to be selected. Therefore the functional data was split into two parts before single-session ICA was performed. The separate outputs were then compared for a measure of split-half validity; only components displayed in both parts were considered to be valid. Only components displayed by every subject were included in the group analysis. Averages were calculated on the probability maps with a one-sample *t*-test using permutation-based nonparametric inference (Nichols and Holmes, 2002). Subsequently *t*-values were converted to *z*-values and statistical images were thresholded using clusters determined by $Z > 3.719$ and a (corrected) cluster significance threshold of $P = 0.0001$ (Worsley et al., 1992).

Cluster peaks were identified for each component and each subject separately. For the first four maxima of each component map timelines were calculated as described in the following: Before the extraction of the signal from one voxel the following pre-processing was applied; motion correction using MCFLIRT (Jenkinson et al., 2002); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Smith, 2002); spatial smoothing using a Gaussian kernel of FWHM 5.3 mm; mean-based intensity normalization of all volumes; high pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 54.0$ seconds). Registration to an MNI reference brain was carried out using FLIRT (Jenkinson and Smith, 2001; Jenkinson et al., 2002). The extracted raw time course was up-sampled to a temporal resolution of 0.1 second, applying linear interpolation. Then average timelines were computed from the signal following the stimulus onsets of one condition. The onset vectors comprised either onsets of videos, onsets of imitation or onsets of delay periods and were separated into onsets related to abstract movements and onsets related to object-related gestures. Onset vectors for the delay periods were additionally split into four delay durations (<3 seconds, 3–5 seconds, 5–7.5 seconds, and >7.5 seconds) with equal numbers of events. Trials from the observation condition were included in all onset vectors

apart from the onsets of imitation. Percent signal change was calculated relative to the first second after stimulus and timelines after null events were subtracted from timelines after events (Burock et al., 1998). Finally the grand mean of every timeline was computed by averaging over subjects.

RESULTS

Behavioural Results

On average 3.7 trials (SD = 2.6) out of 120 trials were rated as “imitated incorrectly” by at least one rater. The minimum number of trials excluded was 0, the maximum 10.

fMRI Results From Independent Component Analysis

Four similar components were identified in each subject, which were valid in both parts of the split data. The group data can be seen in Fig. 2. Maxima are listed in Table I.

The first component was mainly focused on the occipital lobule, extending into parietal and temporal areas (Fig. 2A). One branch of activation reached from primary visual cortex, to secondary visual cortices in the occipital gyrus including BA17, BA18, BA19 and further ventrally to posterior mid- and inferotemporal areas (near BA37) and also to anterior inferotemporal areas (BA20). The other branch extends more dorsally into the posterior parietal lobule.

The second component present in all subjects (Fig. 2B) comprised the primary sensorimotor areas, with activation far more prominent in the left hemisphere than in the right. The next activation centers were within the supplementary motor area (SMA) reaching into the paracentral lobule (M1), and the presupplementary motor area (pre-SMA). A further local maximum was displayed bilaterally at the superior temporal gyrus (STG). A cerebellar activation could be identified at in the right anterior lobe. Also the posterior midtemporal gyrus showed significant activation. Additional activations could be found bilaterally at the superior parietal lobule and at BA44/45, the latter with a larger activation pattern on the right hemisphere which also extended to BA6. A further local maximum could be identified in the putamen.

The third component to be identified in all subjects had four major activation areas (Fig. 2C). The first one was in the anterior cingulate gyrus, and covered several areas including BA10 extending into BA12. A second focus nearby was on the superior frontal gyrus in the region of medial BA8. The third region displaying large activation was located on the posterior cingulate gyrus and the posterior precuneus, also including several areas such as the posterior part of BA24, BA23 and BA31. The last active regions appeared bilaterally along the intraparietal sulcus and the superior temporal sulcus.

The last component to be found in all subjects also comprised several activated areas (Fig. 2D). This component displays a widespread activation pattern on both hemispheres. The most prominent activation was located along the superior parietal cortex, comprising central and medial BA7. The next activated area was located bilaterally in the posterior cingulate gyrus superior to the splenium of the corpus callosum in BA23. A further area prominent in the pattern was an activation along the anterior cingulate sulcus. The last activated area was more pronounced in the right hemisphere and covers a large area of the prefrontal cortex, extending from near BA6 to BA46, and on the right side even further into the lateral prefrontal cortex (BA10).

Timeline Results

The timelines from the four maxima in each component correlated above $r = 0.95$ ($P < 0.05$).

Therefore only the timeline from the overall maximum was further analyzed for each component. The timeline from component 1 displayed the highest maximum after video presentations (2.55 and 2.63% signal change for abstract gestures and object-related actions, respectively). Neither maxima nor time-to-peak differed between conditions. The timeline from component 2 reached maximal values after imitation cues (5.69 and 6.53% signal change, respectively). These maxima differed significantly between conditions, so that component 2 displayed a higher activity after object-related actions as compared to abstract gestures ($P < 0.001$). There was no difference between conditions in regard to the time-to-peak.

In component 3 and 4 maxima were reached after the beginning of delay periods. Furthermore component 3 displayed two local maxima for both conditions. Times to peak were analysed with regard to on and offset of delay periods.

The first peak in component 3 seemed to be onset-locked, although the time-to-peak was slightly earlier in the shortest as compared to the second shortest delay period ($P = 0.03$, corrected). The second peaks displayed no difference between delay period durations if they were compared after the end of delay periods ($F_{2,14} = 0.013$, $P = 0.989$, Greenhouse-Geisser-corrected), thus it can be interpreted as locked to the offset of the delay-period. There was no difference between conditions in regard to the time-to-peak; however, maxima of the first peak were higher after object-related actions as compared with abstract gestures ($F_{1,14} = 10.28$, $P = 0.006$).

Component 4 again displayed only one peak, which seemed to be locked to the offset of the delay period, as there again was no difference of times-to-peak between the delay period durations when compared after the end of the delay-period ($F_{2,14} = 0.99$, $P = 0.406$).

This peak was dependent on condition and could only be observed before the imitation of object-related actions ($F_{1,14} = 11.49$, $P = 0.004$).

Figure 2.

The four networks identified by independent component analysis ($Z > 3.719$) and percent signal change within the maxima of each component after related onsets. **(A)** Visual perception network with timelines after onset of videos. **(B)** Motor preparation and execution network with timelines after signal to imitate. **(C)** Motor working memory (encoding and retrieval)

network with timelines after onset of delay period. **(D)** Object-related activation of affordances also with timelines after onset of delay period. Time courses are depicted for both conditions (A–D) and for four different delay period durations (C and D, length of the delay period indicated by colored square).

DISCUSSION

Aim of the present study was to identify the underlying neural networks that process the different aspects of imitation. Furthermore we wanted to explore the processing of object-related actions as compared with abstract gestures.

Four independent networks were active during delayed imitation. We propose that these four networks represent the aspects of (1) action perception, (2) motor preparation and action execution, (3) encoding and retrieval into and from motor working memory, as well as (4) the dynamic integration of object affordances into actions.

TABLE I. MNI coordinates, maximum Z value of the local maxima for the four components: (1) action perception, (2) motor preparation and action execution, (3) encoding and retrieval into and from motor working memory (4) dynamic integration of object affordances

Component	Coordinates (MNI)			Z-max
	x	y	z	
1				
L. lateral occipital cortex	26	-82	24	7.62
R. lateral occipital cortex	-24	-78	26	5.67
L. inferior lateral occipital cortex	-24	-86	-6	6.19
R. intracalcarine cortex	8	-76	2	5.67
L. occipital fusiform gyrus	-30	-70	-14	5.49
2				
L. primary sensorimotor area	-46	-28	8	6.27
R. primary sensorimotor area	46	-34	58	4.63
Supplementary motor area (SMA)	0	-28	52	5.90
Presupplementary motor area (preSMA)	-2	-6	48	5.40
L. superior temporal gyrus	-56	-28	8	6.27
R. superior temporal gyrus	56	-26	16	5.31
R. cerebellum (anterior lobe)	20	-54	-20	6.11
R. posterior midtemporal gyrus	56	-44	2	5.90
R. superior parietal lobule	40	-50	64	6.47
L. superior parietal lobule	-36	-38	54	5.43
R. inferior frontal gyrus (BA 44/45)	46	6	0	4.59
L. inferior frontal gyrus (BA 44/45)	-48	-2	6	4.14
R. precentral gyrus (BA 6)	54	10	30	4.49
L. putamen	-12	-22	6	4.89
R. putamen	10	22	6	4.73
3				
Anterior cingulate gyrus (BA 10)	0	42	6	5.91
Frontal pole (BA 12)	0	58	16	6.33
Posterior cingulate gyrus (BA 24)	0	-24	38	5.88
Posterior cingulate gyrus (BA 23)	6	-44	26	6.09
Precuneus	2	-52	12	5.98
R. intraparietal sulcus	56	-60	26	5.38
L. intraparietal sulcus	-46	72	30	4.80
R. inferior lateral occipital cortex	56	-62	10	5.85
L. superior temporal sulcus	-54	-32	-2	5.17
R. superior temporal sulcus	60	-40	-4	4.36
4				
R. superior parietal cortex (BA 7)	30	-76	52	6.38
L. superior parietal cortex (BA 7)	-40	-66	42	4.75
Posterior cingulate gyrus (BA 23)	6	-54	30	4.64
Anterior cingulate gyrus	0	24	42	5.09
R. middle frontal gyrus (BA 6)	40	10	32	5.68
R. middle frontal gyrus (BA 46)	44	26	26	5.85
L. middle frontal gyrus (BA 46)	-36	22	24	4.63
R. lateral prefrontal cortex (BA 10)	36	50	16	5.53
L. lateral prefrontal cortex (BA 10)	-34	54	12	5.15

The areas activated above threshold in the first network resembled the two pathways for visual processing (Goodale and Milner, 1992). The connection of the two branches lies in V1 and V2. From there the first branch extended into the visual area V4 and further into the inferior temporal lobe, thereby forming the ventral stream of visual processing. The other branch of activation extended from V1 and V2 into the dorsomedial area, V5, and the inferior pa-

rietal lobe—areas which have been assigned to the dorsal stream of visual processing. In both hemispheres the dorsal branch extended into the superior parietal lobe. The activated areas have been associated with the transformation of sensory inputs into a common coordinate system for action (Lewis, 2006).

Whereas the ventral stream plays an important role in object representations the dorsal stream is associated with

action coding, representation of object locations, and control of the eyes and arms (Goodale and Milner, 1992), therefore both streams can be associated with the watching of the videos in this task.

Indeed, the connection of the activation pattern with the presentation of videos is backed by the timelines, since highest percent signal change in the maximum voxels followed the presentation of visual stimuli.

The second network is clearly related to motor execution as the activation pattern displays the primary sensorimotor cortex (SM1) and the supplementary motor area (including SMA proper and pre-SMA). All further activation sites of that network are also related to imitation as they are described regularly in various movement and imitation studies. The inferior parietal cortex (IPL) plays an important role in imitation (Hermsdörfer et al., 2001; Lewis, 2006; Muhlau et al., 2005; Tanaka et al., 2001). This is connected to findings in relation to ideomotor apraxia, where patients with lesions to the inferior parietal cortex are less able to imitate meaningless gestures (Goldenberg and Karnath, 2006). Activation in the posterior midtemporal gyrus is prominent in this network as well as in the first network described. There it can be associated with the perception of motion pictures; here this activation is likely to be connected to motion perception while subjects watched their hands. The dual assignment of one area to two components can be explained by the dissociation of time courses being independent of the spatial overlap.

Cerebellum is an integrative part of the motor network, it is suggested to play a role in multijoint movement control, and putamen is involved in the execution of skilled movements (Choi et al., 2001). Both are also reported to be involved in initiation and execution of actions, respectively (Krams et al., 1998).

One of the most crucial areas connected to hand actions is the ventral premotor cortex (vPMC). Especially, Brodman's area 44 (BA44) has been reported to play a role in the control of complex actions, such as grasping (Decety et al., 1997; Ehrsson et al., 2001) and imitation of grasping (Grezes and Decety, 2001). It has been specified to be active during goal oriented imitation (Heiser et al., 2003; Iacoboni et al., 1999; Koski et al., 2002), in copying hand (Krams et al., 1998) and finger movements (Tanaka and Inui, 2002) as well as imitation of key sequences (Heiser et al., 2003). However, there are studies that suggest that BA44/45 may not be crucial to imitation itself, but rather to the execution of delayed motor tasks (Makuuchi, 2005; Rushworth et al., 2001). Indeed, the dual assignment of the PMC to this component as well as the fourth component suggests that the activation in BA44/45 cannot be solely explained by the area's involvement in imitation, but was also in part caused by the delay in the task.

The contralateral dorsal premotor cortex (dPMC) displays no activation above threshold. While the vPMC is involved in visuomotor transformations elaborating the appropriate pattern of activation of muscles online, the dPMC seems to play a role in preparation and sequencing

of movement only (Davare et al., 2006). This might explain why it does not appear in an independent component together with the actual execution. In favor of this interpretation is the activation pattern of the third network, which displays dPMC activation as described below.

The third network contains activation clusters in areas known to be connected with action planning and motor working memory. The posterior cingulate has been associated with working memory functions for complex movements (Petit et al., 1998), and the superior parietal cortex possibly stores "pragmatic" action-orientated object descriptions (Buccino et al., 2001; Binkofski et al., 1999), probably with a right hemispheric predominance for object discrimination and a left hemispheric dominance for information maintenance (Stoeckel et al., 2004). Two other areas combining motor working memory and action planning are preSMA and PMC, which play an important role in action planning, but have also been reported to be active during memory delays (Krams et al., 1998; Petit et al., 1998; Toni et al., 1999). Other regions also active in this network, the temporo-occipital transition zone and the inferior temporal gyrus, possibly participate in the temporal storage of motion perception (Bisley et al., 2004).

Compared to the areas that interweave working memory and action planning, this network also includes areas which have been clearly assigned to working memory, such as the dlPFC, which plays a role in maintenance and manipulation of working memory contents (D'Esposito et al., 1999) and the intraparietal sulcus, which shows activity independent of action preparation (Roth et al., 2006; Thoenissen et al., 2002). The bilateral activation of the vlPFC could be assigned to either motor preparation and/or working memory, as it has been reported to play a role in both aspects (Courtney et al., 1998; Simon et al., 2002). The observed differences between conditions (abstract gestures and object-related actions) in timelines from the maxima replicate the findings from Koski et al. (2002) which showed higher activation in action planning areas associated with goal-directed actions. Nevertheless, the activation in both conditions is substantial; hence the network as a whole plays a role in delayed imitation, independent of the involvement of an object. Interestingly, all four timelines which were computed for the different lengths of the delay period show a dual-peaked shape of signal change (see Fig. 2). As the first peak is locked to the onset of the delay period and the second peak is locked to the offset of the delay period, we suggest this pattern can be explained by encoding into and retrieval from working memory.

Maintenance of actions within motor working memory might then be reflected by the plane between the two peaks in the signal of the third network, since some of the areas display more activation for maintenance compared to manipulation, e.g. the right precentral gyrus, the ventrolateral prefrontal cortex (D'Esposito et al., 1999), or the left superior parietal lobe (Stoeckel et al., 2004).

The last network is notable for its interesting spatial pattern of activations, and particularly for the time course of

its signal. This network is activated differently between conditions, being inactive during the delay period after the presentation of abstract gestures, but reaching a definite maximum at the end of the delay period after object-related actions, or, more specifically, shortly before a possible imitation of the object-related actions has to be executed.

As object feature integration should occur during the perception of objects (i.e. within the first network) we suggest a different interpretation of this network, namely the call of affordances towards the object. Ellis and Tucker (2000) proposed that the representation of a visually presented object includes not only a description of its visual properties, but also of relevant motor components. Related activations have been reported for the dPMC, the superior parietal lobe, the superior temporal sulcus (Grezes et al., 2003; Mecklinger et al., 2002) and the posterior cingulate (Mecklinger et al., 2002)—regions which also display significant activity in this fourth network. The question remains whether affordances are triggered immediately during the perception of an object or only in the case of an intention to act on it (Arbib, 1997; Grezes et al., 2003). ICA is able to identify regions that are activated at the same time, and the time course analysis from the maxima can be used to relate these networks to aspects of the task. Therefore our findings can shed new light onto the dynamic process of implementing object affordances into object-related actions. Our data show that the integration of affordances is time-locked to the offset of the delay period. It therefore occurs between perception (component 1) and action (component 2) at the end of the delay period and at a time, when also action planning (component 3) is also processed, shortly before action execution takes place. The detached integration of object affordances into the perception-to-action process by a separate network supports the notion that objects are processed independently. This suggests that also deficits in object-processing are not necessarily linked to perceptual or motor processing chains.

Three main conclusions can be drawn from these findings. First, delayed imitation is processed by at least three networks. One for perception, including object feature integration, one for motor execution, including motor sequence programming, and one for the encoding and retrieval of information into motor working memory. In our task these networks are supported by a fourth network, which becomes active for the dynamic integration of object affordances into actions. Second, at least two of these networks participate in action preparation, one contains areas connected to working memory and one includes areas, which are connected to the true action execution. This provides supporting evidence for the idea that the disturbance of different domains of motor behaviour in apraxia can be caused by several disruptions of the interface between cognition and motor control.

Last, the dynamic integration of object affordances is rather connected to motor preparation and the following action execution than to perception. Therefore it is not the

presentation of an object but the intention or possibility to act upon an object that is the prerequisite for the activation of the fourth network. Furthermore, the processing of objects can be, at least partly, separated from perceptual and motor processing.

ACKNOWLEDGMENTS

The authors thank Joachim Hermsdorfer for his helpful comments on the manuscript, and Katrin Mueller and Kathrin Wendt for their support with acquiring the fMRI data.

REFERENCES

- Arbib MA (1997): From visual affordances in monkey parietal cortex to hippocampo-parietal interactions underlying rat navigation. *Philos Trans R Soc Lond B Biol Sci* 352:1429–1436.
- Beckmann C, Smith S (2004): Probabilistic independent component analysis for functional magnetic resonance imaging. *IEEE Trans Med Imaging* 23:137–152.
- Bekkering H, Wohlschlagel A (2002): Action perception and imitation: A tutorial. In: Prinz W, Hommel B, editors. *Common Mechanisms in Perception and Action*, Vol. XIX: Attention and Performance. Oxford, UK: Oxford University Press. pp 294–314.
- Bekkering H, Wohlschlagel A, Gattis M (2000): Imitation of gestures in children is goal-directed. *Q J Exp Psychol A* 53:153–164.
- Biederman I (1987): Recognition-by-components: A theory of human image understanding. *Psychol Rev* 94:115–147.
- Binkofski F, Buccino G, Posse S, Seitz R, Rizzolatti G, Freund H (1999): A frontoparietal circuit for object manipulation in man: Evidence from an fMRI-study. *Eur J Neurosci* 11:3276–3286.
- Bisley J, Zaksas D, Droll J, Pasternak T (2004): Activity of neurons in cortical area MT during a memory for motion task. *J Neurophysiol* 91:286–300.
- Buccino G, Binkofski F, Fink G, Fadiga L, Fogassi L, Gallese V, Seitz R, Zilles K, Rizzolatti G, Freund H (2001): Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *Eur J Neurosci* 13:400–404.
- Buccino G, Vogt S, Ritzl A, Fink G, Zilles K, Freund H, Rizzolatti G (2004): Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron* 42:323–334.
- Burock M, Buckner R, Woldorff M, Rosen B, and Dale A (1998): Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *Neuroreport* 9:3735–3739.
- Choi S, Na D, Kang E, Lee K, Lee S, Na D (2001): Functional magnetic resonance imaging during pantomiming tool-use gestures. *Exp Brain Res* 139:311–317.
- Churchill A, Hopkins B, Ronqvist L, Vogt S (2000): Vision of the hand and environmental context in human prehension. *Exp Brain Res* 134:81–89.
- Comon P (1994): Independent component analysis, A new concept? *Signal Processing* 36:287–314.
- Courtney SM, Petit L, Maisog JM, Ungerleider LG, Haxby JV (1998): An area specialized for spatial working memory in human frontal cortex. *Science* 279:1347–1351.

- Davare M, Andres M, Cosnard G, Thonnard J, Olivier E (2006): Dissociating the role of ventral and dorsal premotor cortex in precision grasping. *J Neurosci* 26:2260–2268.
- Decety J, Grezes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F (1997): Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120:1763–1777.
- D'Esposito M, Postle B, Ballard D, Lease J (1999): Maintenance versus manipulation of information held in working memory: An event-related fMRI study. *Brain Cogn* 41:66–86.
- Ehrsson H, Fagergren E, Forssberg H (2001): Differential fronto-parietal activation depending on force used in a precision grip task: An fMRI study. *J Neurophysiol* 85:2613–2623.
- Ellis R, Tucker M (2000): Micro-affordance: The potentiation of components of action by seen objects. *Br J Psychol* 91:451–471.
- Goldenberg G, Karnath H (2006): The Neural Basis of Imitation is Body Part Specific. *J Neurosci* 26:6282–6287.
- Goodale M, Milner A (1992): Separate visual pathways for perception and action. *Trends Neurosci* 15:20–25.
- Gibson JJ (1977): The theory of affordances. In: Shaw R, Brandford J, editors. *Perceiving, Acting, and Knowing: Toward an Ecological Psychology*. Hillsdale, NJ: Erlbaum. pp 67–82.
- Greenwald A (1970): Sensory feedback mechanisms in performance control: With special reference to the ideo-motor mechanism. *Psychol Rev* 77:73–99.
- Grezes J, Decety J (2001): Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Hum Brain Mapp* 12:1–19.
- Grezes J, Tucker M, Armony J, Ellis R, Passingham RE (2003): Objects automatically potentiate action: An fMRI study of implicit processing. *Eur J Neurosci* 17:2735–2740.
- Habeck C, Rakitin B, Moeller J, Scarneas N, Zarahn E, Brown T, Stern Y (2005): An event-related fMRI study of the neural networks underlying the encoding, maintenance, and retrieval phase in a delayed-match-to-sample task. *Brain Res Cogn Brain Res* 23:207–220.
- Heiser M, Iacoboni M, Maeda F, Marcus J, Mazziotta J (2003): The essential role of Broca's area in imitation. *Eur J Neurosci* 17:1123–1128.
- Hermesdörfer J, Goldenberg G, Wachsmuth C, Conrad B, Ceballos-Baumann AO, Bartenstein P, Schwaiger M, Boecker H (2001): Cortical correlates of gesture processing: Clues to the cerebral mechanisms underlying apraxia during the imitation of meaningless gestures. *NeuroImage* 14:149–161.
- Hyvarinen A (1999): Fast and robust fixed-point algorithms for independent component analysis. *IEEE Trans Neural Netw* 10:626–634.
- Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G (1999): Cortical mechanisms of human imitation. *Science* 268:2526–2528.
- Jackson PL, Meltzoff AN, Decety J (2006): Neural circuits involved in imitation and perspective-taking. *Neuroimage* 13:429–439.
- Jenkinson M, Bannister P, Brady M, Smith S (2002): Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage* 17:825–841.
- Jenkinson M, Smith S (2001): A global optimisation method for robust affine registration of brain images. *Med Image Anal* 5:143–156.
- Johnson SH, Grafton ST (2003): From 'acting on' to 'acting with': The functional anatomy of object-oriented actions schemata. *Prog Brain Res* 142:127–139.
- Koch G, Oliveri M, Torriero S, Carlesimo G, Turriziani P, Caltagirone C (2005): rTMS evidence of different delay and decision processes in a fronto-parietal neuronal network activated during spatial working memory. *Neuroimage* 24:34–39.
- Koski L, Iacoboni M, Dubeau M, Woods R, Mazziotta J (2003): Modulation of cortical activity during different imitative behaviors. *J Neurophysiol* 89:460–471.
- Koski L, Wohlschläger A, Bekkering H, Woods R, Dubeau M, Mazziotta J, Iacoboni M (2002): Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb Cortex* 12:847–855.
- Krams M, Rushworth M, Deiber M, Frackowiak R, Passingham R (1998): The preparation, execution and suppression of copied movements in the human brain. *Exp Brain Res* 120:386–398.
- Leung H, Gore J, Goldman-Rakic P (2002): Sustained mnemonic response in the human middle frontal gyrus during on-line storage of spatial memoranda. *J Cogn Neurosci* 14:659–671.
- Leung H, Oh H, Ferri J, Yi Y (2007): Load response functions in the human spatial working memory circuit during location memory updating. *Neuroimage* 35:368–377.
- Lewis J (2006): Cortical networks related to human use of tools. *Neuroscientist* 12:211–231.
- Makuuchi M (2005): Is Broca's area crucial for imitation? *Cereb Cortex* 15:563–570.
- Mecklinger A, Gruenewald C, Besson M, Magnie MN, von Cramon DY (2002): Separable neuronal circuitries for manipulable and non-manipulable objects in working memory. *Cereb Cortex* 12:1115–1123.
- Muhlau M, Hermesdörfer J, Goldenberg G, Wohlschläger A, Castrop F, Stahl R, Rottinger M, Erhard P, Haslinger A, Ceballos-Baumann AO, Conrad B, Boecker H (2005): Left inferior parietal dominance in gesture imitation: An fMRI study. *Neuropsychologia* 43:1086–1098.
- Nichols T, Holmes A (2002): Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Hum Brain Mapp* 15:1–25.
- Petit L, Courtney S, Ungerleider L, Haxby J (1998): Sustained activity in the medial wall during working memory delays. *J Neurosci* 18:9429–9437.
- Roth J, Serences J, Courtney S (2006): Neural system for controlling the contents of object working memory in humans. *Cereb Cortex* 20:1595–1603.
- Rumiati R, Tessari A (2002): Imitation of novel and well-known actions: The role of shortterm memory. *Exp Brain Res* 142:425–433.
- Rushworth M, Krams M, Passingham R (2001): The attentional role of the left parietal cortex: The distinct lateralization and localization of motor attention in the human brain. *J Cogn Neurosci* 13:698–710.
- Simon S, Meunier M, Pietre L, Berardi A, Segebarth C, Bous-saoud, D (2002): Spatial attention and memory versus motor preparation: Premotor cortex involvement as revealed by fMRI. *J Neurophysiol* 88:2047–2057.
- Smith S (2002): Fast robust automated brain extraction. *Hum Brain Mapp* 17:143–155.
- Stoeckel M, Weder B, Binkofski F, Choi H, Amunts K, Pieperhoff P, Shah N, Seitz R (2004): Left and right superior parietal lobule in tactile object discrimination. *Eur J Neurosci* 19:1067–1072.
- Tanaka S, Inui T (2002): Cortical involvement for action imitation of hand/arm postures versus finger configurations: An fMRI study. *Neuroreport* 13:1599–1602.

- Tanaka S, Inui T, Iwaki S, Konishi J, Nakai T (2001): Neural substrates involved in imitating finger configurations: An fMRI study. *Neuroreport* 12:1171–1174.
- Thoenissen D, Zilles K, Toni I (2002): Differential involvement of parietal and precentral regions in movement preparation and motor intention. *J Neurosci* 22:9024–9034.
- Tipper SP, Paul MA, Hayes AE (2006): Vision-for-action: The effects of object property discrimination and action state on affordance compatibility effects. *Psychon Bull Rev* 13:493–498.
- Toni I, Schluter N, Josephs O, Friston K, Passingham R (1999): Signal-, set- and movement-related activity in the human brain: An event-related fMRI study. *Cereb Cortex* 9:35–49.
- Toni I, Shah N, Fink G, Thoenissen D, Passingham R, Zilles K (2002): Multiple movement representations in the human brain: An event-related fMRI study. *J Cogn Neurosci* 14:769–784.
- Volle E, Pochon J, Lehericy S, Pillon B, Dubois B, Levy R (2005): Specific cerebral networks for maintenance and response organization within working memory as evidenced by the “double delay/double response” paradigm. *Cereb Cortex* 15:1064–1074.
- Worsley K, Evans A, Marrett S, Neelin P (1992): A three-dimensional statistical analysis for CBF activation studies in human brain. *J Cereb Blood Flow Metab* 12:900–918.