Neural Mechanisms Underlying Freedom to Choose an Object

Markus Thimm,^{1,2*} Ralph Weidner,¹ Gereon R. Fink,^{1,3} and Walter Sturm²

¹*Institute of Neuroscience and Medicine (INM-3), Cognitive Neurology Section, Research Centre Jülich, Germany*

²*Section Clinical Neuropsychology, Department of Neurology, University Hospital RWTH Aachen, Germany*

³*Department of Neurology, University Hospital Cologne, Germany*

Abstract: Previous brain imaging studies identified the neural networks underlying free choice of self-initiated actions. In contrast, the neural mechanisms underlying free choice of external objects remain to be elucidated. In this event-related functional magnetic resonance imaging study, participants had to choose one out of two different single-colored target squares presented at two of three possible locations. In 50% of the trials the choice was either free or specified, which was indicated by a preceding cue. In order to disentangle processes associated with object choice from those related to motor responses, object-response mapping was orthogonally varied. Processes related to the freedom of choice were isolated by means of an adaptive algorithm: based on the subjects individual choices in the free trials, specified trials were continuously generated in a way that matched the free trials in all aspects but the freedom to choose the object. Comparing free and specified trials revealed enhanced neural activity of a bilateral symmetrical network including the dorsolateral prefrontal, medial frontal, and medial parietal cortex. This network overlaps with that shown previously to be associated with free motor selection. It includes the pre-supplementary motor area (pre-SMA), suggesting that this area is rather associated with a supramodal function of initiating choice than with a specific motor function. Neural activity specifically associated with the freedom to choose an object was found bilaterally in the lateral superior parietal cortex. A psychophysiological interaction (PPI) analysis showed increased functional connectivity of this area with bilateral areas of the extrastriate visual cortex. *Hum Brain Mapp* 33:2686–2693, 2012. © 2011 Wiley Periodicals, Inc.

Key words: fMRI; free choice; internal generation; perceptual choice; action selection; decision making; prefrontal cortex; pre-SMA; superior parietal lobule

INTRODUCTION

The “free will” of a person has been characterized by two aspects: the “internal generation” and the “choice between alternative possible actions” [Haggard, 2005]. Based on Descartes, dualistic positions assumed that the mind generates the choice and consecutively causes the brain to initiate the selected action. However, this concept is incompatible with modern neuroscientific findings which conversely suggest that conscious experiences are consequences of brain activity. According to this perspective, the brain decides “on its own” when and how to act

Contract grant sponsor: Deutsche Forschungsgemeinschaft;
Contract grant number: DFG-KFO 112.

*Correspondence to: Markus Thimm, Institute of Neuroscience and Medicine (INM-3), Cognitive Neurology Section, Research Centre Jülich, Wilhelm-Johnen-Strasse, 52425 Jülich, Germany. E-mail: mthimm@ukaachen.de

Received for publication 13 July 2010; Revised 2 February 2011; Accepted 31 May 2011

DOI: 10.1002/hbm.21393

Published online 20 September 2011 in Wiley Online Library (wileyonlinelibrary.com).

Figure 1.

fMRI task; examples of free and specified trials with preceding color or location cue.

while, nevertheless, the person itself has the impression of a freely chosen action. This results in the fundamental question which brain areas are involved in generating a decision that a person perceives as being “free”? Before this issue can be addressed, the underlying concept of freedom has to be clarified: we consider a decision to be free when a choice from two or more alternatives is not constricted by any explicit law, rule, or instruction and neither involves a reward nor a penalty. Otherwise the decision is biased by external factors, becomes predictable at least to a certain degree, and with increasing predictability it must be regarded as decreasingly free. Thus, the concept of freedom underlying the present experiment is not absolute but gradual and in our experiment, we tried to maximize subject’s degrees of freedom. The freedom to choose, of course, is limited by the experimental conditions to the set of possible targets. However, within the frame of the experimental constraints, the choice can be considered as free.

Previous brain imaging studies which investigated the neural correlates of free decisions differed with regard to the content of what had to be chosen. Studies set their focus on the free choice of self-initiated actions [Cunnington et al., 2002; Deiber et al., 1991, 1999; Frith et al., 1991; Gerardin et al., 2004; Jenkins et al., 2000; Lau et al., 2004b; Nachev et al., 2005; Rowe et al., 2005; Soon et al., 2008] or task performance [Forstmann et al., 2006; Haynes et al., 2007; Walton et al., 2004] and it remains to be clarified whether the observed neural processes are specific for the respective context or can be generalized to perceptual non-motor tasks, too.

To the best of our knowledge, to date, the neural mechanisms underlying the free choice of an external object as an isolated perceptual cognitive process, i.e., uncoupled from any motor activity, are unknown. A neural network underlying the “freedom of choice” in a more general sense, i.e., irrespective of the content to be chosen, is expected to overlap with brain areas involved in choosing an action. However, one can also expect that some brain areas are specifically associated with the free choice of an external object as opposed to the choice of an internally initiated action since both brain processes differ fundamentally concerning the criteria “perception”/“action” and “outside world”/“inner world”. Using functional magnetic resonance imaging (fMRI) in healthy volunteers, we investigated the neural correlates of the freedom to choose an object.

MATERIALS AND METHODS

Subjects

Twenty-eight right-handed healthy volunteers participated in the experiment (11 females/17 males). The median age was 25.5 years (range 21–55 years). All subjects gave informed consent prior to the experiment. The study protocol was approved by the local ethics committee according to the declaration of Helsinki.

fMRI Activation Tasks

In an event-related fMRI paradigm (see Fig. 1) subjects had to choose one out of two different monochrome (red,

yellow, or blue) target squares (size: 2.3°) presented at two of three possible locations (left = -3.2° , central = 0° , right = $+3.2^\circ$) at the horizontal centerline of a gray colored screen. Dependent on the relationship between a preceding cue and the two target squares, in 50% of a total of 216 trials the choice was free, and in the remaining 50% of trials it was specified. In each trial, prior to the presentation of the targets a cue was displayed. This was a monochrome square—identical to the targets—which was presented vertically displaced 4.8° above one of the three possible target locations, which were highlighted by three white placeholder squares during presentation of the cue. In different trials either the color of the cue or its location contained the information relevant for the task. The German words for “color” or “location” at the beginning of each of 12 alternating blocks indicated which of these aspects was currently relevant and valid for a whole block of 18 trials. In the color condition, subjects had to attend to the color of the cue. If one of the subsequent target squares matched the cue-color they were obliged to choose that one (specified choice), if not, subjects could freely choose between the two target squares (free choice). Likewise, in the location condition subjects were obliged to choose any target square appearing at the corresponding location as the cue (specified choice) or otherwise (if there was no target at the corresponding location) to choose freely between the two targets. The two different cue types allowed to control for a systematic effect of cue modality (color/location) on subsequent processes related to free choices of a target.

The choice of a target was carried out via three response buttons. The assignment of the response buttons to the target squares changed randomly from trial to trial and was indicated by an icon displayed below each target square. This ensured a separation of object choice and motor response, i.e., the decision to choose the left, central, or right square was not confounded by pressing the left, central, or right response button. Additionally, the hand of response was counter-balanced across subjects to exclude any lateralization effect of motor response.

Cue squares were presented for 1,000 ms and target squares for 2,000 ms. The interstimulus interval (ISI) between cue and targets was 0 ms. After pressing a response button the chosen target square was highlighted by a black frame for 500 ms, giving the subject a feedback of his/her choice. If by mistake a response button was pressed which was not assigned to a target square, or if there was no button press within 1500 ms, a maroon horizontal warning stripe was overlaid on the target squares for 500 ms, indicating an error. Following the presentation of the colored target squares the three white placeholder squares were shown for 2000 ms before the next trial started.

Each block contained nine free choice and nine specified choice trials presented in a pseudo-randomized order. Beginning with the third block, a matching procedure started which was continued until the end of the experiment.

Adapted to the previous choices in the free trial condition, those specified trials were presented (in random order) which matched exactly the previous free trials in terms of color, location, and choice of the target squares as well as assignment of the response buttons. Likewise, specified targets from the first two blocks were tried to be matched by identical free targets. However, since there was no control over the choice in the free condition, the matching in this case was only guaranteed for color and location of the targets but not for the choice. Therefore, from each subject in the end a few trial pairs had to be discarded where the free choice was not identical with the previous specified choice. Thus, finally for each participant, we compared two exactly matched conditions (“free” versus “specified”) which only differed by the freedom of choice.

After the experiment, subjects were asked to freely report how they performed the free decisions and whether they used any implicit rule or strategy.

fMRI Data Acquisition

fMRI was performed on a 3-T Trio magnetic resonance imaging system (Siemens, Erlangen, Germany) using a T2*-weighted echo planar imaging (EPI) sequence (time repetition = 2,200 ms, time echo = 30 ms; flip angle = 90°). The activation task was presented in an event-related fMRI design. A total of 633 volumes were acquired, each consisting of 30 axial slices, allowing for whole-brain coverage. Slice thickness was 3 mm and interslice distance 0.3 mm, with a 20-cm field of view, 64×64 image matrix.

Statistical Analysis of the fMRI Data

Statistical analysis of the fMRI data was carried out using statistical parametric mapping software (SPM5, Wellcome Department of Imaging Neuroscience, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>) using MATLAB version 7.7 (The Mathworks Inc., Natick, MA). After discarding the first four volumes, functional images were realigned to the new first scan to correct for interscan movement, synchronized to the middle slice to correct for differences in slice acquisition time and normalized to a standard EPI template based on the MNI (Montreal Neurological Institute) reference brain [Ashburner and Friston, 2005; Collins et al., 1998; Evans et al., 1994] using the “unified-segmentation” function in SPM5. This algorithm is based on a probabilistic framework that permits image registration, tissue classification, and bias correction to be combined within the same generative model. The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move the subject’s data into the space of the MNI tissue probability maps [Evans et al., 1994] were then combined with the deformation field transforming between “MNI tissue probability maps” and the MNI single-subject template. The resulting deformation was subsequently applied to the individual EPI

TABLE I. Regions of increased neural activity

Free > specified choice							
TC			Region	BA	Side	RS	z-value
x	y	z					
−6	−72	56	Superior parietal lobule	7	L,R	2096	6.96
−4	16	48	Medial frontal gyrus	8	L,R	238	5.62
−40	24	32	Middle frontal gyrus	9	L	622	5.99
−40	48	10		46	L	25	4.93
44	32	26			R	158	5.85
−34	2	62		6	L	168	5.14
30	2	64			R	44	5.39
−34	20	−2	Inferior frontal gyrus	47	L	166	5.65
38	20	0			R	49	5.04
−36	52	18	Superior frontal gyrus	10	L	17	5.13

TC: Talairach coordinates; BA: Brodmann area; RS: region size (number of voxels, cluster size ≥ 10).

volumes. Finally, all images were smoothed with a Gaussian kernel of 8 mm full-width half-maximum. Two onset regressors were defined for (1) free and (2) specified choice trials. The hemodynamic response to each different event type was modeled using a canonical synthetic hemodynamic response function. The 6 head movement parameters were included as confounds. A first level linear contrast was calculated, comparing events of free versus specified choice. This contrast was taken to the second level, and a random effects analysis was performed with a predefined threshold of $P < 0.05$ FWE (family wise error)-corrected. Only clusters comprising at least 10 voxels are reported and projected onto a SPM template.

Psychophysiological Interaction Analysis

In order to get further insight into the network underlying free choice, we calculated a psychophysiological interaction (PPI) analysis [Friston et al., 1997] investigating the functional connectivity of those brain areas underlying free choice (relative to specified choice). PPI analysis was performed by extracting signal time series from a sphere (6 mm) centered at subject specific activation coordinates. For each subject these seed regions were determined by selecting the local activation maximum closest to the overall group maximum. To generate a PPI-regressor, the extracted time course was multiplied with a vector coding free choices, where free choice trials were coded 1 and all other elements were coded 0. The PPI regressor was subsequently convolved with a hemodynamic response function. Such a PPI regressor was generated for each subject and each seed region, respectively. First level statistical analyses were performed by generating and estimating a model involving the PPI as a regressor. Subject-specific contrast images were generated by applying a t -contrast that was 1 for the PPI regressor and 0 elsewhere. Subsequently, a second-level random effects analysis was performed on these contrast images using a one sample t -test.

Results are reported at a corrected significance level of $P < 0.05$.

RESULTS

Behavioral Results

For each subject error trials were determined and discarded. Trials were defined as erroneous when subjects pressed the button that was assigned to neither of the two targets or when they chose a “wrong” target, i.e., when they did not adhere to the instruction for a specified trial. The mean error rate was 3.0 (± 3.0)% for specified trials and 3.7 (± 3.9)% for free trials. For each condition (specified/free), the mean from the subject’s median response times was calculated. Mean reaction times for specified trials (666 ± 66 ms) were faster ($T = 12.3$; $P < 0.001$) than for free trials (818 ± 110 ms).

fMRI Data

To determine activations associated with freedom of choice, we investigated the contrast “free > specified” (see Table I and Fig. 2). Free choice in contrast to specified choice was associated with enhanced neural activity of a bilateral symmetrical frontoparietal network including the middle frontal gyrus (BA 6, 9, 46), inferior frontal gyrus (BA 47), medial frontal gyrus with a local maximum in the pre-SMA (BA 8), superior parietal lobule (BA 7), and the left superior frontal gyrus (BA 10). No differences were found for the reverse contrast (specified > free).

Comparing the “free > specified” networks separately for the color cue and the location cue condition ([free > specified]_{color} vs. [free > specified]_{location}) did not reveal any differences in neither direction, even when lowering the threshold for significance to $P < 0.001$ uncorrected.

The free reports about implicit rules or strategies revealed that each subject performed the task according to

Figure 2.

Lateral and medial view of the contrast “free > specified choice”, $P < 0.05$ family wise error (FWE)-corrected.

the instruction, i.e., they first selected a square based on its color or location and afterwards regarded the corresponding icon code.

PPI Analysis

The PPI analysis was performed for the three main activation clusters of the free > specified network: BA 7, 8, and 9 (see Table I and Fig. 2). Increased functional connectivity during free choice (compared to specified choice) was found only for the seed region in the superior parietal lobule (BA 7), resulting in a left occipital cluster (TC-34, -69, -15; $P < 0.05$ FWE-corrected). Since this cluster comprised only 2 voxels, for illustrative purposes, we analyzed the data again using the more liberal FDR-correction. This analysis showed increased functional connectivity with occipital areas including BA 18 (bilaterally) and right BA 19 (see Table II and Fig. 3). The PPI analysis of frontal areas (BA 8 and 9) did not show any significant results.

TABLE II. PPI analyses ($P < 0.05$ FDR corrected)

Free > specified choice seed region BA 7								
TC			Region	BA	Side	RS	z-value	
x	y	z						
-34	-69	-15	Lingual gyrus	18	L	191	4.88	
32	-80	-13	Fusiform gyrus	19	R	64	4.49	
32	-63	-12	Lingual gyrus	18	R	183	4.39	

TC: Talairach coordinates; BA: Brodmann area; RS: region size (number of voxels, cluster size ≥ 10).

Figure 3.

PPI analysis; “free > specified choice”, seed region BA 7, $P < 0.05$ false discovery rate (FDR)-corrected.

DISCUSSION

In contrast to previous studies that investigated the neural correlates of free choice, the design of our experiment ensured a dissociation of target choice and motor response, i.e., the decision to choose a left, middle, or right object was disentangled from pressing the left, middle, or right response button. Furthermore, the set of specified choice trials was selected individually for each subject based on previous free choice trials. An adaptive algorithm selected specified choice trials such that visual input and choice of the targets as well as the button presses were identical in the free and the specified condition. Thus, finally for each participant we compared two exactly matched conditions of free versus specified choice of a visually perceived object, which allows us to relate any differential neural activity to the freedom to choose an object.

Reaction times in the free choice condition were significantly slower than in the specified choice condition. In previous functional imaging studies, some authors have regarded slower reaction times as a problem since this could argue for a higher task difficulty in one condition and thus confound the results in the sense that the identified networks might simply track task difficulty. However, we opine that fMRI studies do not reflect “task difficulty” itself but the physiological correlate of the cognitive process which is required to solve a task. Thus, if one contrasts a more difficult with a less difficult task, one isolates those brain regions/networks which represent the additional cognitive process that is necessary to solve the more difficult compared to the less difficult task. Transferred to our study this means: the free condition was more difficult than the specified condition because it required the additional process of internal generation of a decision (which was exactly the intended matter of our study).

The neural correlates of this cognitive process were located in a distinct bilateral fronto-parietal network including the dorsolateral prefrontal cortex (DLPFC) and the medial frontal and parietal cortex. These areas have previously been shown to be associated with free choice of an action [Cunnington et al., 2002; Deiber et al., 1991, 1999; Frith et al., 1991; Gerardin et al., 2004; Jenkins et al., 2000; Lau et al., 2004b; Nachev et al., 2005; Rowe et al., 2005; Soon et al., 2008]. Our study shows that activation of these areas also holds true for a purely perceptual free choice, independent from grasping, pointing or any other selection of a motor response. Therefore, one can conclude that these areas represent a general neural network underlying the “freedom of choice.”

Interestingly, the pre-supplementary motor area (pre-SMA) of the medial frontal cortex was part of this network, although it is usually regarded as a motor related area [Nachev et al., 2008; Picard and Strick, 1996] or as a neural correlate for attention to the intention to act [Lau et al., 2004a]. According to the response-conflict theory [Botvinick et al., 2001], the pre-SMA plays a crucial role whenever a choice between incompatible actions is required which results in a response conflict and an inhibition of one response in favor of another [Garavan et al., 2003; Nachev et al., 2005, 2007; Rushworth et al., 2002; Ullsperger and von Cramon, 2001]. The results of our study are compatible with this response-conflict model regarding the aspect of conflict. However, our results suggest that the function of the pre-SMA is not specifically related to a suppression or choice of a motor response. It rather represents a choice conflict on a superordinated level and might be regarded as a neural correlate of a task independent center of free choice. This notion is supported by a study from Taylor et al. [2008] who showed that medial frontal structures including the pre-SMA were activated when subjects freely chose where to attend. The results are also in line with a study by Lau et al. [2006] who showed that free choice of a motor activity was associated with the pre-SMA while response conflict activated a more ventral cluster in the anterior cingulate cortex (ACC). Accordingly, our study involved free visual choice which did not cause response conflict. Consistently, the activation cluster of the medial cortex extended from the pre-SMA into the mid-cingulate cortex, but did not reach the ACC [WfU Pickatlas; Maldjian et al., 2003]. This supports the view that ACC might be specifically involved when decisions are concerned with a motor response and is furthermore supported by a study of Walton et al. [2004] who found the ACC activated when subjects freely decided what action to make.

Other consistently reported areas in association with free choice of action are located at the lateral surface of the frontal cortex, in particular the DLPFC (BA 9/46) [Deiber et al., 1991; Frith et al., 1991; Jenkins et al., 2000; Lau et al., 2004b]. Rowe et al. [2005] found this area activated by free selection not only of motor responses but also of colors. However, the authors themselves noted that it was not

guaranteed (albeit likely) that participants in fact chose a color since it was possible to disregard instructions and perform the task regardless of colors by just selecting a finger movement to press a button. Our results now strengthen the notion of Rowe et al. [2005] that—beside the pre-SMA—the DLPFC is part of a superordinated network of free choice regardless of modality, i.e., associated with the selection of any kind of action and perception. Likewise, areas of the medial and lateral prefrontal cortex have previously been shown by Haynes et al. [2007] to be associated with freely chosen intentions.

The cognitive process underlying free choice of perceived stimulus material should not be confounded with the concept of selective attention or covert spatial orientation. These attention processes require a matching of an external perception with an internal representation or with a rule that prescribes a location or quality of a stimulus that should be attended or suppressed. Importantly, in our experiment, selective attention and covert spatial orientation were equally required in both, the free and specified condition (attending to a defined location or color of the target given by the preceding cue) and therefore subtracted from each other. Thus any difference in neural activity we found cannot be ascribed to selective attention or covert spatial orientation. In contrast, the cognitive process we measured represents an internal generation of a decision initiated by freedom of choice. The conceptual difference between covert spatial orientation (as in the study by Taylor et al. [2008]) and selecting an external object (as in our study) might be the reason for differences in the underlying neural networks. Lateral prefrontal activation was only found when selecting an object but not for covert spatial orientation.

We also found neural activity specifically associated with the freedom to choose an object. This was located bilaterally in BA 7 of the superior parietal lobule (SPL). It was more extended to the lateral surface than has been reported by studies of free motor choice. This is a plausible result since the SPL is part of a network which is known to bias the competition among multiple stimuli for representation in visual cortex [Kastner and Ungerleider, 2000] and to be involved in the top-down control of visual stimulus selection [Corbetta and Shulman, 2002].

However, not any kind of visual selection process seems to activate the SPL in the same way. In the study by Taylor et al. [2008], who investigated the free selection of where to orient visual spatial attention, the SPL was not activated. In contrast to that study, in our experiment the selection process did not only comprise orienting of spatial attention but also the selection of an object that could have been done by other than spatial criteria, particularly by the color of the object. This experimental difference might be crucial for the activation of the SPL. Specific activation of the SPL was also found in a study by Nee and Jonides [2009] when performing perceptual selection but not in the memorial selection task. One might conclude that activity of the SPL in a free choice task represents the interaction

with the “outside world” and the processing of an object in order to select it. In contrast, motor selection, memorial selection, or spatial orientation can be done without stimulus processing which might be the reason for the missing neural activity of the SPL in those tasks. This is supported by the results of our PPI analysis, showing functional connectivity patterns during free choice between the SPL and areas of the visual cortex—a plausible neural correlate of the free visual selection process.

Limitations

One might argue that the effects which we ascribe to the freedom of a decision might be confounded by differences in the preceding cue/target matching process: detecting a match of cue feature/position and target feature/position in the specified condition may in principle comprise a target detection which was not present in the free condition (possibly resulting in a prolonged search process). However, this notion implies that participants performed the matching task by exclusively focusing on the cued location (or color) and coming to a present/absent decision solely based on this information, thus ignoring additional information available in the display. In principle, a free trial was signaled by both the absence of a feature/position match and by the presence of two non-matching items (e.g., a red cue followed by the presence of a yellow and blue item). In order to optimize their performance, subjects presumably used all available information. A stronger involvement of target detection in the specified relative to the free condition should be reflected by activation within a specific network of brain areas. However, the “specified > free” contrast did not show any significant neural activation, supporting the view, that subjects used all available information and that target detection was comparable in free and specified trials.

Another critical aspect relates to spatial attentional reorienting subsequent to the matching process. This might have occurred differentially in the location cue condition since after presentation of the cue, attention was possibly focused on the cued location and then had to be reoriented in free choice trials. However, since such a spatial focusing was not possible in the color cue condition and a comparison between location and color cue condition did not show any differential effect between the activated neural networks, it is unlikely that attentional reorienting processes played a crucial role and confounded the differential activation between free and specified trials.

The interpretation of our results is strictly limited to our concept of freedom. From other philosophical points of view, one might argue that even “free” choices are still restricted since rules or instructions may be implicit. We do not deny that implicit rules or instructions may bias the decision. However, according to our definition, the degree of freedom solely depends on the absence of explicit constraints. Implicit rules would belong to the internal gen-

eration process and be part of the free decision. A free decision does not necessarily have to origin from “nothing” and can be based on implicit rules without contradicting our definition of freedom. In contrast to other definitions, our concept is compatible, e.g., with the experiments of Libet et al. [1983] and the view of free will as an illusion, since it does not make any assumptions about free agency, i.e., it does not postulate that one could have decided otherwise, but rejected that option.

CONCLUSIONS

In summary, we investigated neural correlates of the internal generation of a free decision. In contrast to previous studies, the decision in our experiment was related to perceptual choice disentangled from motor choice. Our network of freedom to choose an object overlaps with the networks of selection and internal generation of an action as reported by previous studies. It includes the pre-SMA and the DLPFC, suggesting that these areas have a rather supramodal function than a specific motor function in tasks where free choice is required. Furthermore, our network contains specific activity of the lateral SPL which is normally not found as a neural correlate of the free selection of action. This result suggests that the internal generation of free choice at least partly differs on the neural level when choosing an external object as opposed to an internally planned action.

ACKNOWLEDGMENTS

Authors are grateful to their colleagues from the Interdisciplinary Centre for Clinical Research (IZKF), University Hospital RWTH Aachen, for their technical support, and to the Cognitive Neurology group of the Institute of Neuroscience and Medicine, Research Centre Jülich, for many stimulating discussions.

REFERENCES

- Ashburner J, Friston KJ (2005): Unified segmentation. *Neuroimage* 26:839–851.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD (2001): Conflict monitoring and cognitive control. *Psychol Rev* 108:624–652.
- Collins DL, Zijdenbos AP, Kollokian V, Sled JG, Kabani NJ, Holmes CJ, Evans AC (1998): Design and construction of a realistic digital brain phantom. *IEEE Trans Med Imaging* 17:463–468.
- Corbetta M, Shulman GL (2002): Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215.
- Cunnington R, Windischberger C, Deecke L, Moser E (2002): The preparation and execution of self-initiated and externally-triggered movement: A study of event-related fMRI. *Neuroimage* 15:373–385.
- Deiber MP, Passingham RE, Colebatch JG, Friston KJ, Nixon PD, Frackowiak RS (1991): Cortical areas and the selection of movement: A study with positron emission tomography. *Exp Brain Res* 84:393–402.

- Deiber MP, Honda M, Ibanez V, Sadato N, Hallett M (1999): Mesial motor areas in self-initiated versus externally triggered movements examined with fMRI: Effect of movement type and rate. *J Neurophysiol* 81:3065–3077.
- Evans AC, Kamber M, Collins DL, MacDonald D (1994): An MRI-based probabilistic atlas of neuroanatomy. *Magn Reson Scan* 264:263–274.
- Forstmann BU, Brass M, Koch I, von Cramon DY (2006): Voluntary selection of task sets revealed by functional magnetic resonance imaging. *J Cogn Neurosci* 18:388–398.
- Friston KJ, Buechel C, Fink GR, Morris J, Rolls E, Dolan RJ (1997): Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage* 6:218–229.
- Frith CD, Friston K, Liddle PF, Frackowiak RS (1991): Willed action and the prefrontal cortex in man: A study with PET. *Proc Biol Sci* 244:241–246.
- Garavan H, Ross TJ, Kaufman J, Stein EA (2003): A midline dissociation between error-processing and response-conflict monitoring. *Neuroimage* 20:1132–1139.
- Gerardin E, Pochon JB, Poline JB, Tremblay L, Van de Moortele PF, Levy R, Dubois B, Le BD, Lehericy S (2004): Distinct striatal regions support movement selection, preparation and execution. *Neuroreport* 15:2327–2331.
- Haggard P (2005): Conscious intention and motor cognition. *Trends Cogn Sci* 9:290–295.
- Haynes JD, Sakai K, Rees G, Gilbert S, Frith C, Passingham RE (2007): Reading hidden intentions in the human brain. *Curr Biol* 17:323–328.
- Jenkins IH, Jahanshahi M, Jueptner M, Passingham RE, Brooks DJ (2000): Self-initiated versus externally triggered movements. II. The effect of movement predictability on regional cerebral blood flow. *Brain* 123 (Part 6):1216–1228.
- Kastner S, Ungerleider LG (2000): Mechanisms of visual attention in the human cortex. *Annu Rev Neurosci* 23:315–341.
- Lau HC, Rogers RD, Haggard P, Passingham RE (2004a) Attention to intention. *Science* 303:1208–1210.
- Lau HC, Rogers RD, Ramnani N and Passingham RE (2004b) Willed action and attention to the selection of action. *Neuroimage* 21:1407–1415.
- Lau H, Rogers RD, Passingham RE (2006): Dissociating response selection and conflict in the medial frontal surface. *Neuroimage* 29:446–451.
- Libet B, Gleason CA, Wright EW, Pearl DK (1983): Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. *Brain* 106 (Part 3):623–642.
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003): An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage* 19:1233–1239.
- Nachev P, Rees G, Parton A, Kennard C, Husain M (2005): Volition and conflict in human medial frontal cortex. *Curr Biol* 15:122–128.
- Nachev P, Wydell H, O'Neill K, Husain M, Kennard C (2007): The role of the pre-supplementary motor area in the control of action. *Neuroimage* 36 (Suppl 2):T155–T163.
- Nachev P, Kennard C, Husain M (2008): Functional role of the supplementary and pre-supplementary motor areas. *Nat Rev Neurosci* 9:856–869.
- Nee DE, Jonides J (2009): Common and distinct neural correlates of perceptual and memorial selection. *Neuroimage* 45:963–975.
- Picard N, Strick PL (1996): Motor areas of the medial wall: A review of their location and functional activation. *Cereb Cortex* 6:342–353.
- Rowe JB, Stephan KE, Friston K, Frackowiak RS, Passingham RE (2005): The prefrontal cortex shows context-specific changes in effective connectivity to motor or visual cortex during the selection of action or colour. *Cereb Cortex* 15:85–95.
- Rushworth MF, Hadland KA, Paus T, Sipila PK (2002): Role of the human medial frontal cortex in task switching: A combined fMRI and TMS study. *J Neurophysiol* 87:2577–2592.
- Soon CS, Brass M, Heinze HJ, Haynes JD (2008): Unconscious determinants of free decisions in the human brain. *Nat Neurosci* 11:543–545.
- Taylor PC, Rushworth MF, Nobre AC (2008): Choosing where to attend and the medial frontal cortex: An fMRI study. *J Neurophysiol* 100:1397–1406.
- Ullsperger M, von Cramon DY (2001): Subprocesses of performance monitoring: A dissociation of error processing and response competition revealed by event-related fMRI and ERPs. *Neuroimage* 14:1387–1401.
- Walton ME, Devlin JT, Rushworth MF (2004): Interactions between decision making and performance monitoring within prefrontal cortex. *Nat Neurosci* 7:1259–1265.