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The neural correlates of perceiving one's own movements

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Abstract

Feedforward mechanisms are important for movement control. They may also contribute to the identification of self-produced actions by attenuating the sensory consequences of self-produced movements. In our study, subjects opened and closed their hand slowly and continuously (0.5 Hz). This movement was filmed with an MRI compatible video camera and projected online onto a screen, viewed by the subject while BOLD contrast was measured with fMRI. The temporal delay between movement and feedback was parametrically varied (0–200 ms). In each trial, subjects judged whether there was a delay or not. There was a positive correlation between the extent of the temporal delay and activation in the right posterior superior temporal cortex (pSTS) and a negative correlation in the left putamen. A second analysis addressed the neural correlates of subjective judgement under conditions of uncertainty. This contrast showed a differential activation in the cerebellum. These results support the assumption of a forward model implying that predictions generated in motor areas attenuate sensory areas. They also suggest that efference copy mechanisms are not located within specific brain areas but are implemented as a specific form of interaction between perceptual and motor areas depending on the modalities and the type of actions involved. Further, conscious detection of small temporal deviations might be based on signals generated in the cerebellum which provide fine-grained temporal information. These results might be useful to refine theories about the role of forward mechanisms in the emergence of disorders of the self, such as in schizophrenia.

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Introduction

To control our actions, it is essential to distinguish between events caused by ourselves or another agent. This “attribution” problem may be solved in two different ways. Carrying out goal-directed actions, we intend to produce certain changes in the environment. The perceived changes are compared to the intended changes such that the consequences of self-generated actions are identified (Farrer and Frith, 2002; Georgieff and Jeannerod, 1998; van den Bos and Jeannerod, 2002; Ruby and Decety, 2001; Jeannerod et

al., 2003). A second model claims that during the initiation of a motor program, a prediction of its sensory consequences (efference copy) is generated. This prediction is then compared to the actual sensory consequences (Blakemore et al., 1998; Frith et al., 2000). Originally this mechanism was proposed to account for perceptual constancy, that is, the phenomenal experience of a stable visual world in spite of continuously moving eyes (von Holst and Mittelstaedt, 1950). Recently, the basic assumption behind this idea has been expanded to motor control in general (Haruno et al., 2001; Wolpert et al., 1995).

Prior research in this context addressed the phenomenon that we cannot tickle ourselves (Weiskrantz et al., 1971). Ticklishness ratings increase after introducing a temporal delay between a self-generated movement and its tactile consequences (Blakemore et al., 1999). This implies that the

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prediction of the future consequences of a motor command can modulate tactile sensations. Using functional imaging, it has been shown that there is a positive correlation between the length of the delay (between self-generated movement and its tactile consequences) and the activation of the cerebellum as well as the somato-sensory cortex (Blakemore et al., 1998, 2001). The right anterior cerebellar cortex was selectively deactivated by self-produced movements that resulted in a tactile stimulus and significantly activated by externally produced tactile stimuli (Blakemore et al., 1998). This result has been interpreted as evidence for a forward model mechanism in which the cerebellum provides a signal that modulates the activation of somatosensory areas.

Although recent functional imaging studies have addressed spatial aspects of visuomotor integration (Farrer et al., 2003; see Discussion), the temporal aspects of visuomotor integration have not yet been explored with functional imaging. Analogous to the tactile domain the simultaneousness of producing and observing the same movement is likely to play an important role in perceiving it as self-generated. In our study, subjects opened and closed their hand continuously, while they watched their action on a video screen online. We introduced short temporal delays into the visual feedback and measured correlates of brain activation with fMRI during this task. We investigated whether different temporal delays between carrying out a simple repetitive movement and perceiving the respective visual feedback would change the pattern of activation in brain areas related to motor control and movement perception. In addition, we were interested in signal changes corresponding to the explicit judgments of simultaneity between the movement and its visual consequences.

We hypothesized that visuomotor integration is achieved by a predictive mechanism such as the forward model. Perceptual areas involved in movement processing, such as area MT or the posterior superior temporal sulcus (pSTS) (Grossman et al., 2000; Perrett et al., 1989; Puce and Perrett, 2003) should show an increase in activation with increasing mismatch between actual and observed own movement. Simultaneity between actual and observed movement should lead to an attenuated signal in areas related to movement perception. Areas involved in motor control, such as the basal ganglia, the cerebellum, premotor cortex, or the SMA, should provide the attenuating signal.

Methods

Eighteen healthy right-handed subjects were recruited. After a complete description of the study they gave their written informed consent according to the Declaration of Helsinki. Subjects opened and closed their right hand continuously and smoothly (0.5 Hz) while BOLD contrast was measured with fMRI. In the closing position, the fingers did not touch each other or the palm. All subjects were able to perform the task before the scanning session and inside the

scanner according to the instructions. The hand movements were filmed using an fMRI compatible video camera (Wild et al., 2000) and projected online onto a screen, visible by the subjects via a mirror. This direct visual feedback of the own hand movement was given at random time points for a 3 s duration. During these 3 s trials pseudorandom temporal delays between 0 and 200 ms (40 ms steps) were introduced. The interstimulus interval was jittered between 10 and 14 s (mean 12 s). The subject's task was to decide if a temporal delay was introduced. They indicated their choice after each event by pressing one of two buttons with the left thumb. Online temporal delays of the video feedback were realized by a PC frame grabber card and custom made software. Picture frames were loaded on a ring buffer and reentry occurred at time points between 0 and 200 ms in 40 ms intervals. Between trials, the last image frame was frozen, so that subjects saw their static hand while they continued their movement until the next trial started. A total of 120 trials was performed, i.e., 20 trials at each delay length.

Scanning was performed with a Siemens 1.5 Tesla scanner (Sonata). Functional images consisted of echo-planar image volumes which were sensitive to BOLD contrast (TE 40 ms, TR 2 s, flip angle 90°). The volume covered the whole brain with a 64*64 matrix and 22 slices with in plane resolution of 3*3 mm². Three runs, consisting of 253 volumes, were acquired. To ensure that a steady state magnetization has been reached, the first six acquired volumes were discarded. A trigger signal from the scanner, the button press of the subject, and the onset of the stimuli were registered in a protocol, together with the timeline, on a separate computer. A T1 weighted data set (MP-RAGE; 1.5*1*1 mm³) was collected to serve as an anatomical reference.

For image processing, and all statistical analyses SPM99 (Wellcome Department of Cognitive Neurology, London) was used. The images of each subject were corrected for acquisition delay (slice timing) and were realigned by using the first scan of the block as reference. T1 anatomical images were coregistered to the mean of the functional scans and aligned to the SPM T1 template in the MNI space (Montreal Neurological Institute, mean brain). The calculated nonlinear transformation was applied to all images for spatial normalization. Finally, the images were smoothed with a 12 mm full-width, half-maximum (FWHM) Gaussian filter. A high pass filter with a cutoff period of 40 s and a low pass filter with a cutoff period of 4 s were used. The relationship between delay length and neural activation was calculated in a parametric analysis for each subject in a fixed effect model. The SOAs (stimulus onset asynchronies) from the protocol file were defined as events and convolved with the hemodynamic response function. In this approach events (delay lengths ranging from 0 to 200 ms) were modeled parametrically and contrast images for a positive and for a negative linear correlation calculated for each subject separately. Condition and subject effects were estimated according to the general linear model at each voxel in

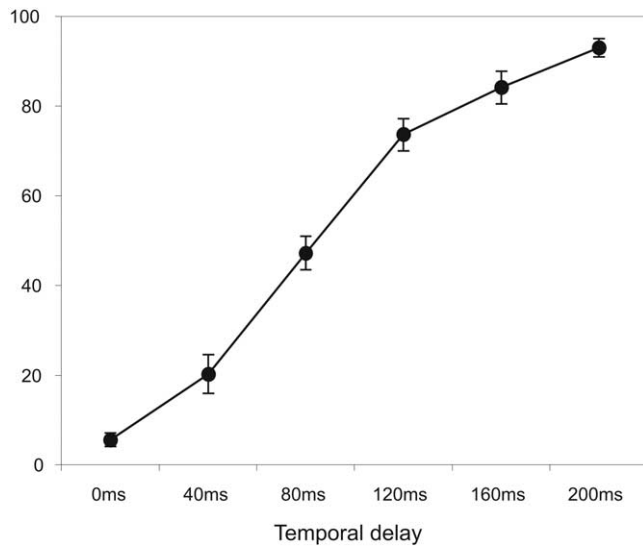


Fig. 1. Perceptual judgments as a function of temporal delay (error bars indicate standard error of the mean). The longer the delay the more often it was recognized. The point of highest uncertainty was close to 80 ms delay.

the brain space. These contrast images were then entered in a second level model (simple *t* test).

Activations are reported if they exceed a threshold of $P < 0.05$ corrected on the cluster level for the parametric contrasts ($P < 0.05$ on the single voxel level for the main effect).

For a second analysis only delay lengths ranging between a 25 and 75% ratio for yes/no delay responses were used. This ratio was chosen, because at these delay lengths subjects were uncertain about their choice. Because a sufficient number of trials (minimum of 40) in each subject was required, only 14 subjects were included in this analysis. For each subject a fixed effect model was defined with one contrast for “no” answers (temporal delay not detected) in the uncertainty range, a second for “yes” answers (temporal delay detected) in the uncertainty range, and a third for all answers outside the uncertainty range (0%–25% and 75%–100%). On a second level simple *t* tests were used to compare “delay detected” minus “delay not detected” and “delay not detected” minus “delay detected.” Activations are reported if they exceeded $P < 0.05$, corrected for multiple comparisons on single voxel and cluster level. A small volume correction was performed for this contrast with a cerebellar mask.

Results

Behavioral data: Simultaneity judgments as a function of delay

Subjects judged whether there was a temporal delay between their movement and the visual feedback or whether

they occurred simultaneously. Fig. 1 shows these judgments as a function of delay. The percentage of “delay recognized” judgments increased with increasing delay.

fMRI data

Areas involved in visuomotor integration and simultaneity judgments

The neural response to the task irrespective of delay length, i.e., visual feedback vs no feedback comprises frontal, temporoparietal, and sensorimotor brain areas (for details see Table 1).

Areas correlated with extent of delay

Activation in a brain area lying in the right posterior superior temporal sulcus at the borders of superior temporal gyrus, middle temporal gyrus, and supramarginal gyrus (MNI x, y, z mm 48, -42, 18; $z = 3.94$; $P = 0.021$, corrected for multiple comparisons) was correlated positively with the delay length (see Fig. 2). Activation in the left putamen (MNI x, y, z mm -27, 3, 3; $z = 4.08$; $P = 0.017$, corrected for multiple comparisons) was negatively correlated with the delay length (see Fig. 3).

Contrast for conscious detection of delay

In a separate analysis we assessed differences between trials where the delay was consciously detected (yes) and trials in which the delay was not consciously detected (no), selectively for trials having a high uncertainty level (25%–75% detection rate). Within this range, the physical differences between different delays were small (40–120 ms). In 14 subjects the range of this uncertainty interval was wide enough to collect a sufficient number of trials for the analysis. In the “yes” minus “no” comparison, conscious detection was correlated with a cerebellar activation (MNI x, y, z ; 3 -72 -30; $z = 4.35$; $P = 0.023$, corrected for multiple

Table 1
Neural activation of all events vs baseline irrespective of delay length

Cerebral area	Brodmann area	Side	MNI			z scores
			x	y	z	
Insula	47	R	33	21	-6	6.23
Inferior frontal gyrus	48	R	54	12	9	6.21
Precentral gyrus	6	R	48	6	36	5.58
Middle temporal gyrus	37	R	51	-69	3	6.11
Superior occipital gyrus	18	R	24	-93	15	5.31
Middle occipital gyrus	17	L	-24	-96	9	5.97
Insula	47	L	-33	21	-6	5.87
Precentral gyrus	6	L	-51	6	36	5.76
Supplementary motor area	32	L	-3	18	48	5.67
Postcentral gyrus	48	L	-54	-24	27	5.43
	3	L	-33	-36	63	5.29
Putamen		L	-15	12	-6	4.95

Note. Activations are reported if $P < 0.05$ corrected on the single voxel level.

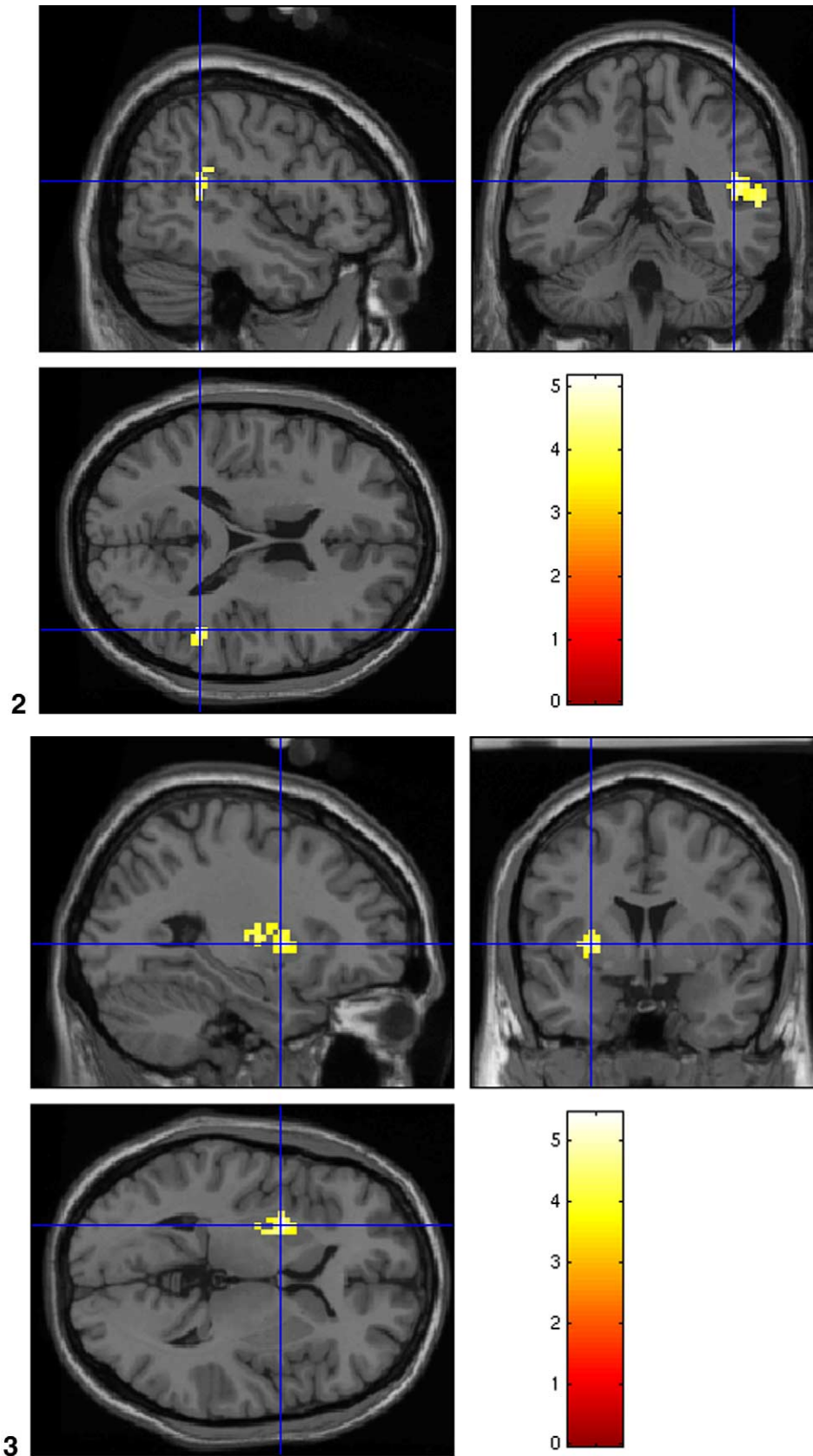


Fig. 2. Positive correlation with the delay length. Maximum intensity projection (MIP) showing voxels in the right superior temporal lobe (pSTS). The contrast images from correlational analysis for each subject individually were entered a second level analysis ($n = 18$).

Fig. 3. Negative correlation with delay length is negatively correlated with the delay length. The above MIP shows an activation in the left putamen.

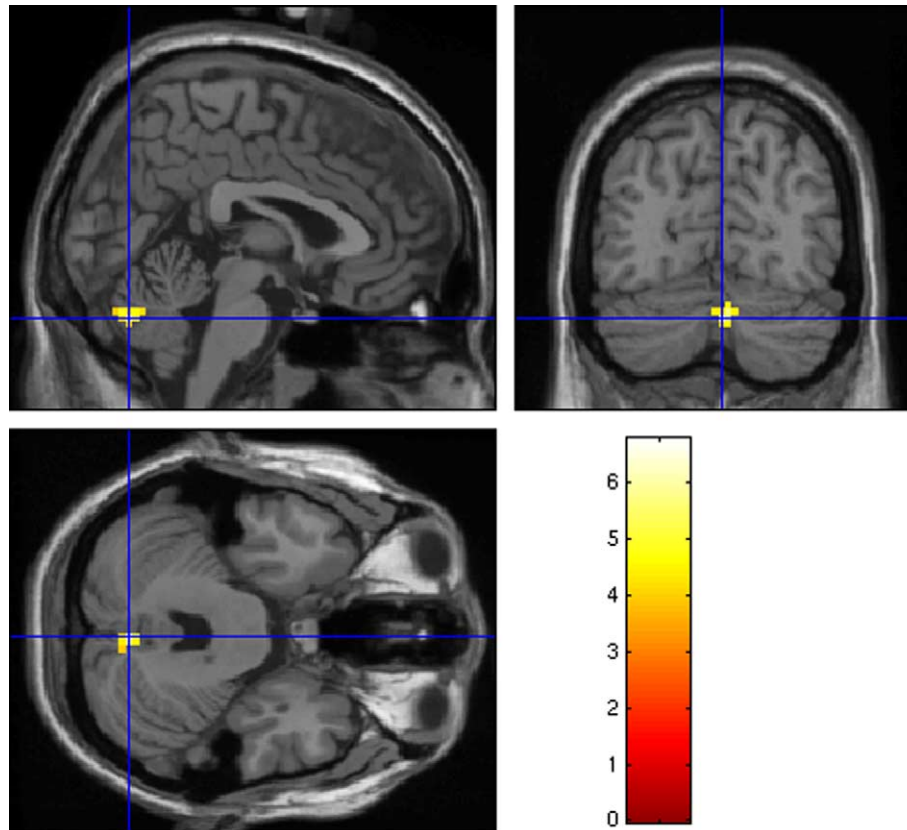


Fig. 4. Subjective ratings with high uncertainty. Results of the differential contrast no-delay vs delay in 14 subjects. Only delay lengths were taken into account that were rated by each subject individually at an a priori defined level of uncertainty.

comparisons, see Fig. 4). There were no significant differences in the “no” minus “yes” comparison.

Discussion

Activation in the posterior superior temporal sulcus (pSTS), a crucial area for movement perception (Grezes et al., 2001; Grossman et al., 2000), was positively correlated with the extent of the temporal delay between a self-generated movement and its visual feedback. Conversely, the activation of a core area for motor control, the putamen (Dreher and Grafman, 2002), was negatively correlated with the temporal delay. This pattern of activation is expected when a motor area generates signals that in turn modulate activation in perceptual areas. Our findings support the assumption that the integration of a movement with its visual consequences may rely on a forward mechanism.

Previous research has shown that the posterior lateral temporal lobe is closely related to movement perception (Perrett et al., 1989; Huk et al., 2002). In particular, the perception of biological movement (point light figures, eyes, and mouth movement) is processed in the posterior superior temporal sulcus (pSTS) (Grezes et al., 2001; Puce and Perrett, 2003), predominantly right lateralized (Gross-

man et al., 2000). The striatum (putamen) is interconnected with various cortical areas by cortico-striatal-thalamic loops (McGeorge and Faull, 1989; Schultz and Romo, 1992). Recent anatomical studies (Yeterian and Pandya, 1998) revealed fiber tracts linking the putamen with superior temporal areas. Thus, signals generated in the putamen might attenuate movement perception areas.

Whereas the present study used temporal delays to address the neural correlates of perceiving one's own movements, earlier studies have used spatial distortions. In particular, a recent PET study (Farrer et al., 2003) used a task first described by Franck et al. (2001). Subjects carried out a joystick movement and visual feedback was provided by a virtual hand. The angular deviation between the observed and actual movement was systematically varied. Activation in the right inferior parietal lobe was positively correlated with the degree of the angular discrepancy. In addition, there was a negative correlation between the angular discrepancy and activation of the insula. This pattern of results is different from the one obtained in the present study. Distinct networks are likely to be involved in perceiving temporal vs. spatial features of one's own movement.

Explicit judgments of simultaneity in our study were correlated with signal changes in the cerebellum. In previous investigations the cerebellum has been shown to pro-

vide a signal for the modulation of somatosensory consequences of movements (Blakemore et al., 2001). Their activation was present in the right anterior cerebellar cortex and decreased when a movement was self-produced. In the present study the cerebellar activation emerged from the medial cerebellar cortex. It occurred when subjects rated a movement as their own, at delay lengths which were ambiguous with respect to the simultaneousness of their movements and the visual consequences resulting from them. The studies with somatosensory stimuli suggest that the cerebellum provides an error signal predicting the sensory consequences of motor commands (Blakemore et al., 1998, 2001). In the present study, however, it rather seemed to be involved in providing fine-grained information about the timing of visual events under conditions of uncertainty. This finding is in line with recent claims (Ivry, 1996; Ivry et al., 2002) that the cerebellum plays a central role in providing accurate timing information. In our experiment, the cerebellar activation might be a correlate of a detection mechanism for small temporal delays that informed explicit simultaneity judgments. More generally, it seems that distinct brain regions provide attenuating signals, depending on the modality under investigation. An attenuation of primary sensory areas (such as the primary sensory cortex in the experiment of Blakemore et al., 1998) is not to be expected in the visual system where attenuation is likely to occur on a higher level (higher visual or associative cortex).

The activation of the lateral prefrontal cortex did not vary with the extent of the delay. This suggests that the mechanism picking up the temporal delay is not based on a comparison of intended and perceived changes in the environment (Decety et al., 2002; Chaminade et al., 2002; Fink et al., 1999). The lack of a putative frontal activation in the present study could be due to repetitive movements requiring little intentional control compared to isolated movements that might require more intentional control. Thus the degree of intentional control needed might have been lower than in studies introducing more meaningful and intended actions (Chaminade et al., 2002; Koski et al., 2002; Frith, 2002). Further intentional control might largely rely on spatial parameters, but does not specify the exact timing parameters of a movement. Thus, the detection of spatial deviations between one's movements and their visual effects might be based on a comparison of intended and perceived changes in the environment, whereas the detection of temporal deviations largely proceeds without contributions of the intentional system.

It has been claimed that impaired forward mechanisms are involved in pathological states such as delusions of influence or passivity experiences in schizophrenia (Kircher and David, 2003; Kircher and Leube, 2003). These patients, especially those with delusions of influence, have difficulties in distinguishing their own from an alien hand carrying out movements under ambiguous experimental conditions (Daprati et al., 1997). In a study by Franck et al. (2001) they found that a similar deficit could be observed when a tem-

poral or angular bias was introduced in the actual visual feedback of a joystick movement that the subjects themselves produced. In particular, patients with delusions of influence showed greater difficulties than those without these symptoms when an angular bias had to be detected. In an earlier PET study (Spence et al., 1997) it has been demonstrated that schizophrenia patients with delusions of influence or passivity phenomena show a hyperactivation of parietal areas that is reduced after symptoms are remitted. This may indicate that the prediction of forward models is corrupted so that the sensory consequences of self-produced movements are not attenuated (Blakemore et al., 2002). Thus the sensory consequences of self-produced movements are at risk of being misclassified as externally generated.

Conclusion

The present study supports the claim that efference copy mechanisms are involved in perceiving one's own movements. It provides evidence for the assumption that activation in a perceptual area, the posterior superior temporal sulcus (pSTS), is attenuated when a movement is carried out and its visual feedback being perceived simultaneously. The attenuating signal might be provided by the putamen, a brain area involved in motor control. This suggests that efference copy mechanisms are not located within specific brain areas but are implemented as a specific form of interaction between perceptual and motor areas. Basic motor signals generated in the cerebellum provide fine-grained timing information that can be used for conscious judgements about synchronicity between movements and their visual consequences.

References

- Blakemore, S.J., Wolpert, D.M., Frith, C.D., 1998. Central cancellation of self-produced tickle sensation. *Nat. Neurosci.* 1, 635–640.
- Blakemore, S.J., Frith, C.D., Wolpert, D.M., 1999. Spatio-temporal prediction modulates the perception of self-produced stimuli. *J. Cogn. Neurosci.* 11, 551–559.
- Blakemore, S.J., Frith, C.D., Wolpert, D.M., 2001. The cerebellum is involved in predicting the sensory consequences of action. *NeuroReport* 12, 1879–1884.
- Blakemore, S.J., Wolpert, D.M., Frith, C.D., 2002. Abnormalities in the awareness of action. *Trends Cogn. Sci.* 6, 237–242.
- Chaminade, T., Meltzoff, A.N., Decety, J., 2002. Does the end justify the means? A PET exploration of the mechanisms involved in human imitation. *NeuroImage* 15, 318–328.
- Daprati, E., Franck, N., Georgieff, N., Proust, J., Pacherie, E., Dalery, J., Jeannerod, M., 1997. Looking for the agent: an investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition* 65, 71–86.
- Decety, J., Chaminade, T., Grezes, J., Meltzoff, A.N., 2002. A PET exploration of the neural mechanisms involved in reciprocal imitation. *NeuroImage* 15, 265–272.

- Dreher, J.C., Grafman, J., 2002. The roles of the cerebellum and basal ganglia in timing and error prediction. *Eur. J. Neurosci.* 16, 1609–1619.
- Farrer, C., Frith, C.D., 2002. Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage* 15, 596–603.
- Farrer, C., Franck, N., Georgieff, N., Frith, C.D., Decety, J., Jeannerod, M., 2003. Modulating the experience of agency: a positron emission tomography study. *NeuroImage* 18, 324–333.
- Fink, G.R., Marshall, J.C., Halligan, P.W., Frith, C.D., Driver, J., Frackowiak, R.S., Dolan, R.J., 1999. The neural consequences of conflict between intention and the senses. *Brain* 122, 497–512.
- Franck, N., Farrer, C., Georgieff, N., Marie Cardine, M., Dalery, J., d'Amato, T., Jeannerod, M., 2001. Defective recognition of one's own actions in patients with schizophrenia. *Am. J. Psychiatry* 158, 454–459.
- Frith, C., 2002. Attention to action and awareness of other minds. *Conscious. Cogn.* 11, 481–487.
- Frith, C.D., Blakemore, S.J., Wolpert, D.M., 2000. Abnormalities in the awareness and control of action. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 355, 1771–1788.
- Georgieff, N., Jeannerod, M., 1998. Beyond consciousness of external reality: a “who” system for consciousness of action and self-consciousness. *Conscious. Cogn.* 7, 465–477.
- Grezes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., Decety, J., 2001. Does perception of biological motion rely on specific brain regions? *NeuroImage* 13, 775–785.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., Blake, R., 2000. Brain areas involved in perception of biological motion. *J. Cogn. Neurosci.* 12, 711–720.
- Haruno, M., Wolpert, D.M., Kawato, M., 2001. Mosaic model for sensorimotor learning and control. *Neural Comput.* 13, 2201–2220.
- Huk, A.C., Dougherty, R.F., Heeger, D.J., 2002. Retinotopy and functional subdivision of human areas MT and MST. *J. Neurosci.* 22, 7195–7205.
- Ivry, R.B., 1996. The representation of temporal information in perception and motor control. *Curr. Opin. Neurobiol.* 6, 851–857.
- Ivry, R.B., Spencer, R.M., Zelaznik, H.N., Diedrichsen, J., 2002. The cerebellum and event timing. *Ann. NY Acad. Sci.* 978, 302–317.
- Jeannerod, M., Farrer, M., Franck, N., Fourneret, P., Posada, A., Daprati, E., Georgieff, N., 2003. Action recognition in normal and schizophrenic subjects, in: Kircher, T., David, A. (Eds.), *The Self in Neuroscience and Psychiatry*, Cambridge University Press, Cambridge, UK.
- Kircher, T.T.J., David, A., 2003. *The Self in Neuroscience and Psychiatry*. Cambridge University Press, Cambridge, UK.
- Kircher, T.T.J., Leube, D.T., 2003. Self consciousness, self agency and schizophrenia. *Consc. Cogn.*, in press.
- Koski, L., Wohlschlagel, A., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., Iacoboni, M., 2002. Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb. Cortex* 12, 847–855.
- McGeorge, A.J., Faull, R.L., 1989. The organization of the projection from the cerebral cortex to the striatum in the rat. *Neuroscience* 29, 503–537.
- Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.J., Hietanen, J.K., Ortega, J.E., 1989. Frameworks of analysis for the neural representation of animate objects and actions. *J. Exp. Biol.* 146, 87–113.
- Puce, A., Perrett, D., 2003. Electrophysiology and brain imaging of biological motion. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 435–445.
- Ruby, P., Decety, J., 2001. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. *Nat. Neurosci.* 4, 546–550.
- Schultz, W., Romo, R., 1992. Role of primate basal ganglia and frontal cortex in the internal generation of movements. I. Preparatory activity in the anterior striatum. *Exp. Brain Res.* 91, 363–384.
- Spence, S.A., Brooks, D.J., Hirsch, S.R., Liddle, P.F., Meehan, J., Grasby, P.M., 1997. A PET study of voluntary movement in schizophrenic patients experiencing passivity phenomena (delusions of alien control). *Brain* 120, 1997–2011.
- van den Bos, B.E., Jeannerod, M., 2002. Sense of body and sense of action both contribute to self-recognition. *Cognition* 85, 177–187.
- von Holst, E., Mittelstaedt, H., 1950. Das reafferenzprinzip (wechselwirkungen zwischen zentralnervensystem und Peripherie). *Naturwissenschaften* 37, 464–476.
- Weiskrantz, L., Elliott, J., Darlington, C., 1971. Preliminary observations on tickling oneself. *Nature* 230, 598–599.
- Wild, B., Erb, M., Lemke, N., Scholz, P., Bartels, M., Grodd, W., 2000. Video camera and light system for application in magnetic resonance scanners. *Magn. Reson. Imaging* 18, 893–896.
- Wolpert, D.M., Ghahramani, Z., Jordan, M.I., 1995. An internal model for sensorimotor integration. *Science* 269, 1880–1882.
- Yeterian, E.H., Pandya, D.N., 1998. Corticostriatal connections of the superior temporal region in rhesus monkeys. *J. Comp. Neurol.* 399, 384–402.