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► **To cite this version:**

Cécile Galléa, Jozina B de Graaf, Mireille Bonnard Bonnard, Jean Pailhous. High level of dexterity: differential contributions of frontal and parietal areas. *NeuroReport*, 2005, 16, pp.1271-1274. hal-01454684

HAL Id: hal-01454684

<https://hal.science/hal-01454684>

Submitted on 22 Nov 2017

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High level of dexterity: differential contributions of frontal and parietal areas

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Received 19 May 2005; accepted 15 June 2005

In the present functional magnetic resonance imaging experiment, study participants performed a dynamic tracking task in a precision grip configuration. The precision level of the force control was varied while the mean force level of 5 N was kept constant. Contrasts cancelling error rate differences between the conditions showed activation of nonprimary motor areas and other frontal structures in response to increasing precision constraints when

the precision of force control could still be increased, and of right primary and associative parietal areas when the precision of the produced force control reached its maximum. These results suggest that the network of frontal and parietal areas, usually working together in fine control of dexterity tasks, can be differentially involved when environmental constraints become very high. *NeuroReport* 16:1271–1274 © 2005 Lippincott Williams & Wilkins.

Key words: Dynamic force control; Functional magnetic resonance imaging; Nonprimary motor areas; Precision grip; Primary motor cortex

INTRODUCTION

The capacity to precisely control low fingertip forces has been acquired in parallel to brain development [1,2]. A specific network of sensorimotor areas seems to be involved in the control of skilled finger movements in humans [3,4]. Frontal nonprimary motor areas [such as ventral and dorsal premotor areas (PMv, PMd), supplementary motor area (SMA), cingulate motor cortex] and the primary motor cortex (M1) compose this network that also extends to the parietal lobe via connections to association areas such as the posterior parietal cortex [5]. The aim of the present study is to better understand the relative contributions of the nonprimary frontoparietal network components and M1 in a specific aspect of dexterity, that is, low force control in thumb–index grip (i.e. the precision grip [6]).

Using functional magnetic resonance imaging (fMRI), Ehrsson and collaborators [3] and Kuitz-Buschbeck and colleagues [7] confirm the implication of the nonprimary frontoparietal network and M1 in the control of precision grip. However, they do not permit insight into the relative contributions of the network components to the *precision* of force control because they either compared different force levels with similar precision demands [3], or covaried precision demands with different tasks [7]. It is known that blood oxygenation-level-dependent (BOLD) activity of several sensory and motor areas, taking part in the nonprimary frontoparietal network of interest, varies with the magnitude of produced muscular force [8–11]. Moreover, both cited studies used static tasks consisting of maintaining a *constant* level of force production, whereas, often, precision grip tasks ask for dynamic force control. Also, it is known that the BOLD signal is less sensitive to static than dynamic force control [11].

In the present fMRI experiment, we studied the relative contributions of the nonprimary frontoparietal network components and M1 in dynamic precision grip force control while the required precision of the control was varied but not mean force level. Because for the highest precision levels the study participants were not always successful, and error is known to influence BOLD signal in some of the regions of interest (for example cingulate areas [12]), we performed specific contrasts that cancelled differences in error rate between precision levels. In that way, we were able to analyse the cerebral network implicated in grip force control with high precision constraints.

MATERIALS AND METHODS

Study participants: Eleven normal, right-handed volunteers (eight men and three women), screened for fMRI compatibility, participated in this study. All participants gave written, informed consent and were paid for their participation. The experiment was approved by the public assistance of Paris Hospitals and the local ethic committee (CCPPRB RBM 01-04).

Experimental design: Participants held a circular force transducer between the thumb and the index finger of the right hand. The produced fingertip forces were online translated into the vertical position of a cursor, placed in the middle of a computer screen. The cursor moved up (down) with the participant's increasing (decreasing) squeezing force. The task goal was to track a force curve passing on the screen with the cursor. The curve was a set of points randomly generated around a 5 ± 2 N value and filtered at 4 Hz (second-order low-pass Butterworth filter), giving the

feeling of an unpredictable curve. We varied the precision level of the force control by using five cursor sizes, representing five conditions: 0.2, 0.3, 0.4, 0.5 and 0.6 N. Each condition, taking 25 s, appeared twice in a session and was never presented twice in a row. The total experiment consisted of five sessions. The order of the conditions was counterbalanced between sessions and participants. The total scanning time was 40 min. The participants were trained for the task 1 week before the fMRI acquisition to ensure stable performance.

Acquisition: The grip forces were sampled at a frequency of 100 Hz by a Labview program. Imaging was carried out with a 3T whole-body Bruker Imager (fMRI centre, Marseille, France). The experience began with the acquisition of a high-resolution structural T1-weighted image for anatomical coregistration (15 min, voxel size $1 \times 0.75 \times 1.22$ mm). The functional images were acquired using a T2*-weighted echo-planar sequence at 20 axial slices (repetition time 1.66 s, interleaved acquisition, slice thickness 3 mm, interslice gap 1 mm, 64×64 matrix of 3×3 mm voxels). The slices, acquired parallel to the anterior commissure–posterior commissure plane, covered the frontal, parietal and occipital lobes. A total of 790 volumes per participant were submitted for analysis.

Analysis: To verify whether the mean force production was similar for all precision levels (i.e. about 5 N), we averaged the force production for each experimental condition over the whole duration of the experiment. To verify whether the participants modified the precision of their force control as a function of cursor size, we calculated the mean distance between the midpoint of the cursor and the required force imposed by the curve-to-track. An adaptation of the force control to higher precision constraints corresponds to less distance between the midpoint of the cursor and the curve-to-track. Finally, we calculated the percentage of time spent by each cursor outside the curve (i.e. the error rate).

Statistical parametric mapping software (spm99) was used for image processing and analysis (<http://www.fil.ion.ucl.ac.uk/spm/>) (for details see [12], except for spatial smoothing $6 \times 6 \times 6$ mm). Data were analysed by modelling the five experimental conditions by a box-car convolved with the haemodynamic response function.

The following T-contrasts between cursor size conditions have been analysed: 0.2–0.6, 0.3–0.6, 0.4–0.6, 0.5–0.6 N. Because the error rate covaried with cursor size, we performed interaction contrasts that cancelled as much as possible the influence of error rate on the differences in BOLD signal obtained in the simple contrasts (see the Results section).

Individual differences between regressor coefficients (or ‘activation differences’) were tested in a random effect analysis. The cluster locations of activation differences are reported using an uncorrected significance threshold for active voxel of either $p=0.001$ for the simple contrasts, or $p=0.01$ for the interaction contrasts. The SPM99 coordinates were converted from MNI (Montreal Neurological Institute) coordinate space to Talairach space and analysed with help of the Talairach atlas [13]. The clusters with an extent of at least 10 voxels (for the simple contrasts) or 5 voxels (for the interaction contrasts) were analysed.

RESULTS

The mean force level produced by the participants was 5 N for all cursor sizes. The precision of force control increased with decreasing cursor size (Fig. 1). Thus, the participants modified the precision of their force control as a function of cursor size. The error rate increased exponentially with the decrease of cursor size (Fig. 1). Comparing cursor 0.2 with 0.3 N, the steep increase in error rate can be explained by the stagnation of the precision of the force control: the precision of the participants’ force control reached its maximum whereas the required precision imposed by the cursor size still increased.

The smallest cursor size condition evoked more activation in several brain structures than the largest one (Fig. 2a, Table 1). The contrast 0.3–0.6 N induced less activity differences (Fig. 2b, Table 1). For the contrast 0.4–0.6 N, only the left SMA proper (SMAp) was found. The contrast 0.5–0.6 N did not show significant activity differences.

In the previous contrasts, the difference in error rate covaried with the difference in required precision of the force control. Therefore, we performed interaction contrasts to cancel as much as possible the effect of error rate. Knowing that the difference in error rate between the cursors 0.2 and 0.3 N was $34.4 - 17.3 = 17.1\%$, and that for 0.3 and 0.6 N $17.3 - 2.3 = 15\%$, we analysed [(0.3–0.6 N)–(0.2–0.3 N)] and [(0.2–0.3 N)–(0.3–0.6 N)]. The first contrast, revealing brain activity related to the precision of grip force control when the precision could still be increased, showed activity in right cingulate areas, bilateral insula, right PMv and PMd, left inferior and superior frontal gyrus, and some foci in left associative sensory areas (green blobs in Fig. 2c, Table 2). The inverse contrast, revealing brain activity related to precision of force control when the level of the produced force precision reached its maximum, even if the precision constraints increased, mainly showed activity in right associative and primary sensory areas (red blobs in Fig. 2c, Table 2).

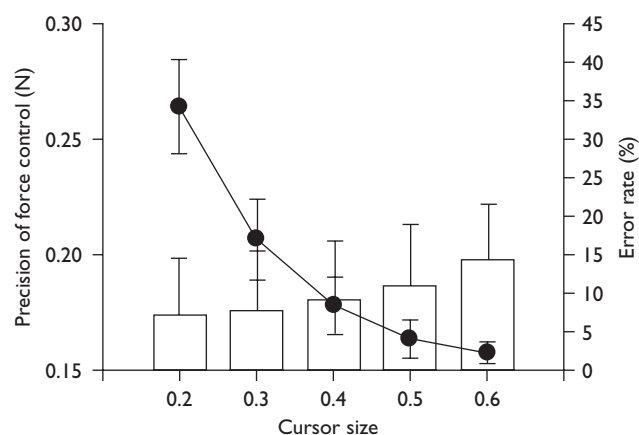


Fig. 1. Behavioural results as a function of cursor size, averaged over all participants. Whiskers indicate standard deviation. Black circles: error rate. The mean error rate was $2.3 \pm 1.4\%$ for the cursor size of 0.6 N, $4.1 \pm 2.6\%$ for 0.5 N, $8.3 \pm 3.9\%$ for 0.4 N, $17.3 \pm 5.3\%$ for 0.3 N and $34.4 \pm 6.1\%$ for 0.2 N. White bars: precision of force control. The mean value for the precision of force control was 0.198 ± 0.024 N for cursor 0.6 N, 0.187 ± 0.027 N for 0.5 N, 0.181 ± 0.025 N for 0.4 N, 0.176 ± 0.025 N for 0.3 N and 0.175 ± 0.024 N for 0.2 N.

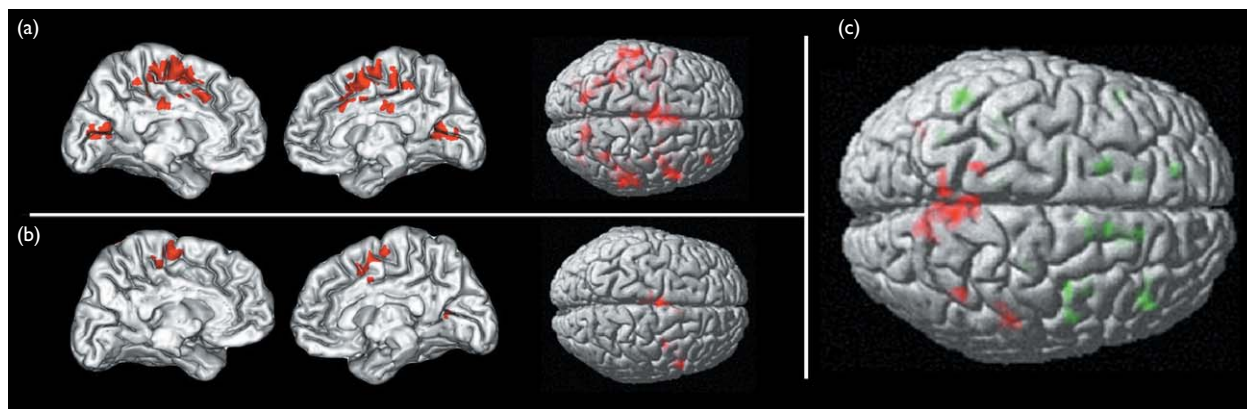


Fig. 2. Activity differences for the contrasts 0.2–0.6 N (a), 0.3–0.6 N (b), and for the interaction contrasts (c) [(0.3–0.6 N)–(0.2–0.3 N)] (green blobs) and [(0.2–0.3 N)–(0.3–0.6 N)] (red blobs). Only activity differences at the surface of the brain are visible. For corresponding anatomical structures, see Tables 1 and 2.

Table 1. Result of contrasts between cursor size conditions.

Cerebral structure	Max Z	x,y,z
<i>0.2–0.6 N</i>		
R inf. parietal lobule (BA 40), R sup. parietal lobule (BA 7), R SI (BA 1, 2, 3)	4.82	28,–56,39
B post. cingulate (BA 23, 30, 31), B cuneus, precuneus (BA 17, 18, 19), R sup. parietal lobule (BA 7), R angular gyrus (BA 39)	4.82	–1,–67,7
R PMv, R sup. and med. frontal gyri (BA 8, 9), R inf. frontal gyrus (BA 44, 46)	4.8	47,11,24
L angular gyrus (BA 39), L inf. parietal lobule (BA 40), L sup. frontal lobule (BA 5, 7), L SI (BA 1,2,3), MI, PMd	4.79	–54,21,22
B SMAp, R pre-SMA, B cingulate gyrus (BA 23, 24, 31), B dorsal ant. cingulate (BA 32)	4.73	–1,0,50
R thalamus	4.67	15,–21,14
R sup. and med. frontal gyri (BA 9,10)	4.41	34,37,25
L PMv, L inf. frontal gyrus (BA 9, 44)	4.32	–51,5,16
L thalamus, L putamen	4.27	–19,–32,6
R MI, R PMd	4.16	31,–18,46
R insula, R inf. frontal gyrus (BA 45)	3.87	28,20,9
<i>0.3–0.6 N</i>		
R post. cingulate (BA 23, 30, 31)	4.62	2,–67,7
R med. and inf. frontal gyri (BA 9, 44, 45)	4.06	47,5,18
L rostral SMAp	4.03	–1,–6,50
L caudal SMAp	3.88	–6,–21,46
R insula	3.87	26,–12,7
R PMd	3.81	34,–6,47
R cingulate gyrus (BA 24), R dorsal ant. cingulate (BA 32)	3.71	4,0,34
<i>0.4–0.6 N</i>		
L SMAp	3.99	–6,–15,52

Cerebral structures underlying the local maxima, in Talairach's reference space: R=right hemisphere; L=left hemisphere; B=bilateral; BA=Brodman's area. See the text for abbreviations of structures.

DISCUSSION

The aim of the present study was to analyse the cerebral network implicated in dynamic precision grip force control in a range comparable to that for fragile object manipulation. At the behavioural level, we have seen that the precision of the force control increased up to a certain level and was stabilized for the highest required precision levels, so that error rate increased steeply. Contrasting different precision level conditions, we found an implication of the

Table 2. Results of the interaction contrasts.

Cerebral structure	Max Z	x,y,z
<i>(0.3–0.6 N)–(0.2–0.3 N)</i>		
R cingulate and sup. frontal gyri (BA 24, 32)	3.99	10,2,39
R insula	3.73	34,2,18
L inf. frontal gyrus (BA 45)	3.24	–46,17,11
L inf. parietal lobule (BA 40)	3.09	–43, 53,39
L insula	3.04	–35, 38,16
L sup. frontal gyrus (BA 8)	2.99	–17,8,45
L med. frontal gyrus (BA 9)	2.85	–14,23,35
R PMv	2.82	44,–3,34
L angular gyrus (BA 39)	2.74	–27, 62,23
R PMd	2.73	31,–6,47
R PMd R. sup. frontal and ant. cingulate gyri (BA 8, 32)	2.6	10,23,41
<i>(0.2–0.3 N)–(0.3–0.6 N)</i>		
B SI, paracentral gyrus (BA 5), R sup. parietal lobule (BA 7)	4.22	5,–56,53
R inf. parietal lobule (BA 40), R SI (BA 2)	3.98	44,–32,35
R inf. parietal lobule (BA 40)	3.52	34,–53,45
R med. temporal gyrus (BA 22), R sup. temporal gyrus (BA 22, 39)	3.08	33,–59,10
L sup. parietal lobule (BA 7)	3.07	–11, 62,55

See legend of Table 1.

nonprimary frontoparietal network, as previous studies on this topic did. However, contrary to these studies [3,7], we were able to attribute changes in BOLD signal to the influence of required precision level. Firstly, we found bilateral M1 significantly more activated in a condition in which the participants controlled their grip force with very high precision relative to the lowest one. This suggests that in a unilateral grip force task, bilateral M1 plays a role in the precision level of the force control. Secondly, when the difference between precision levels decreased, significant activity differences mostly persisted in the left SMAp. Winstein and collaborators [14] also found a role of SMAp in the precision of a movement task. The activity of this area seems to be related to precision level variations of force and

movement control, suggesting a role of SMAp in the motor adaptation to environmental (precision) constraints.

But further to this, the results of the two interaction contrasts, cancelling the error rate differences between the conditions, gave insight into the respective contributions of the nonprimary frontal areas on the one hand, and the associative parietal areas on the other hand. We found nonprimary frontal structures, such as the right middle and anterior part of the cingulate gyrus, right premotor cortex and left inferior and superior frontal gyrus, activated in response to increasing precision constraints but only in a situation in which the precision of the force control could still be increased. Some of these cerebral areas have been found related to action monitoring [15], action planning [14] and motivation to action [16,17]. This strongly suggests that the frontal components of the frontoparietal network, usually found in the fine control of low fingertip forces, are involved in the process of adapting the force control to environmental constraints.

In response to an increase in the precision constraints, even if the precision of the produced force had reached its maximum, we found activity of mainly the right primary (BA 2) and associative parietal areas. It has been suggested that activity in the right intraparietal sulcus is related to additional demands in highly precise sensorimotor control [3]. In a previous study, we also showed that primary and associative sensory areas play an important role in 'sensory awareness' when particular attention has to be paid to the force production [18]. So, this strongly suggests that our most precise cursor size condition was difficult, not because the sensory information could not be processed more 'precisely', but because the force control could not be more precise.

CONCLUSION

In a dexterity task with precision variation of force control, a relationship exists between sensory processing and action monitoring pathways, induced by the task requirements. By increasing precision requirements, which saturated one of the two systems, we were able to show differential contributions of frontal and parietal areas in high dexterity. For a dexterous control with high precision demands, the factors limiting the performance quality can be sensory processes or motor adjustments to adapt the output to the strong requirements of the task. As long as the nonprimary frontal and parietal areas can play their respective roles

together, the quality of the behavioural response can be improved.

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Acknowledgement: This study was performed with grants from the French program Cognition and Information Processing, obtained in collaboration with Prof. Marc Maier. We would like to thank Dr Frédéric Danion for the conception of the behavioural part of the experiment. The experiments were performed in the fMRI Centre of Marseille of which we warmly thank the engineers, especially Bruno Nazarian, for their help. We also thank Dr Jean-Michel Viton who willingly took the medical responsibility for the passage of the participants in the 3 T fMRI machine.