Is perceptual anticipation a motor simulation? A PET study

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A large body of psychophysical evidence suggests that perception of human movement is constrained by the observer's motor competence. PET measurements of regional cerebral blood flow were performed in eight healthy subjects who were requested, in a forced-choice paradigm, to anticipate the outcome of a single moving dot trajectory depicting the beginning of either mechanical, pointing, or writing movements. Selective activation of the left premotor cortex and of the right intraparietal sulcus was associated with visual anticipation of pointing movements while the left frontal operculum and superior parietal lobule were found to be activated during anticipation of writing movements. These results are discussed in the perspective that the motor system is part of a simulation network, which is used to interpret perceived actions. *NeuroReport* 12:3669–3674 © 2001 Lippincott Williams & Wilkins.

Key words: Human; Motor anticipation; Neuroimaging; Perceptual anticipation; Simulation

INTRODUCTION

Decades of research have demonstrated that even simplified depiction of human motion, based on point-light displays, is sufficient for observers to recognize not only locomotion or complex actions such as dancing but also the gender of the person, their personality traits and emotions [1,2]. There is also strong evidence that principles of movement planning and execution such as biomechanical constraints of the body [3], relationship between curvature of trajectory and velocity [4], as well as motor anticipation [5,6] have a great influence on stimuli interpretation.

Motor anticipation defines the principle that rules the co-articulation of the different components of a motor sequence. For instance, the grasping of an object is performed faster if the object must be put down on a wide target rather than a narrow one [6]. Similarly, it has been observed that the kinematics of a handwritten letter change as a function of the spatial constraints of the forthcoming letter [5]. The movement duration of an 'l' followed by another 'l' is shorter than when the 'l' is followed by an 'n'. This indicates that the motor system anticipates the following component while producing the movement. Several studies showed that the visual system could use the cinematic cues included in the first component to predict the forthcoming one in handwriting [5] as well as in reaching [6] movement. The kinematics of an ongoing motion carry the imprint of the following unit of motor action, and these characteristics are clues for the identification of the whole event: motor anticipation is mirrored by perceptual anticipation.

There is a large body of evidence suggesting that these perceptual capabilities are not only due to visual experience but also, at least in part, to motor competence [7]. For example, observations of clinical case show that a specific motor dysfunction such as apraxia [8] or dysgraphia [9] leads to specific perceptual deficit. Thus, the perception of human motion could activate the neural motor structures involved in the covert stages of action (i.e. the stages that precedes movement execution). This was observed for primates as well as for human. In monkey premotor cortex mirror neurons fire during the observation and the production of grasping action [10]. In human, functional imaging data demonstrate selective activation of several cortical regions that are engaged in motor control (namely premotor cortex and parietal lobule) during the perception of human movements [11,12]. Interestingly these regions are not found activated when the movements are biomechanically implausible but only when they are biomechanically plausible [13].

Taken together, these results suggest that the perception of biological movement is mediated by implicit knowledge about the way our motor system implements a behavioral objective [4]. Another way of considering this question is to assume that perception of human movement involves a neural simulation of the perceived action [14] and, therefore, entails motor competence.

The aim of our study was to identify the neural

correlates of the perceptual anticipation using a single moving dot which, depending on the experimental conditions, either depicted mechanical, pointing, or writing movements. We used a forced-choice paradigm in which subjects were shown the first component of the trajectory and then asked to decide amongst two possible outcomes. In agreement with the simulation view it is proposed that perceptual anticipation of human action should activate cortical areas specifically involved in the covert stage of the corresponding action. Therefore, in addition to the frontal areas expected to be involved in the decision process [15,16], prediction of the final target size of a sequential pointing movement would engage parietal areas [17] while guessing the likely ending of cursive handwritten letters should activate areas located within the left frontal opercula [18].

SUBJECTS AND METHODS

Participants: Eight healthy right-handed volunteers aged 18–28 years (mean 22 ± 2.8) gave their informed consent to participate in the experiment, which was approved by the local Ethics Committee (Centre Léon Bérard). The experimental protocol was conducted according to the declaration of Helsinki.

Conditions and stimuli: All stimuli consisted of a black dot movement on a white screen depicting different trajectories. The stimulus used for pointing anticipation (PA) were based on real two-phases pointing movements, in which a first pointing is made to an intermediate 1.5 cm diameter target and the second, to a small or a large final target. For the writing anticipation (WA), dot movements were based on the cursive handwriting of either the couple 'll' or 'ln'. Stimuli for these two conditions were based on human motion, and were prepared with a large sample of pointing and handwriting movements recorded on a digitizer (Wacom Intuos A3; sampling frequency, 200 Hz; spatial resolution, 0.2 mm). As expected on the basis of previous observations [5,6], the characteristics of the second component, small (0.5 cm) or large (2 cm) final target in PA, and 'l' or 'n' second letter in WA, influenced the kinematic aspects of the first sequence, the pointing to the intermediate target for PA (Fig. 1a) and the first letter of the couple in WA (Fig. 1b). In PA, the first sequence duration was longer for the small final target (stimulus duration 885 ± 39 ms) than for the large final target (stimulus duration 748 ± 35 ms). The relative duration of the deceleration phase was also higher for the small than the large target. Similarly, in WA the velocity profile and overall duration of the first letter writing varied between 'll' (stimulus duration 846 ± 26 ms) and 'ln' (stimulus duration 965 ± 32 ms), the main difference concerning the duration of the down stroke part of the first 'l'. Eleven recordings representative of the mean performance were selected in order to preserve the variability in the pointing and writing events used as stimuli.

Dot movements in the object motion condition (OM) were based on a spring-driven ball motion that bounced on a cushion. The distance traveled after bouncing could either be long or short depending on the first impulse given by the spring (30 and 20 cm/s respectively). In both cases, the velocity was modulated by a constant deceleration of 11 cm/s. The same amount of initial trajectory was presented for the long (stimulus duration 850 ms) and short (stimulus duration 1150 ms) and distance. Lastly, the baseline condition (BA) consisted of a dot appearing either on the upper or the lower part of the screen (stimulus duration 900 ms).

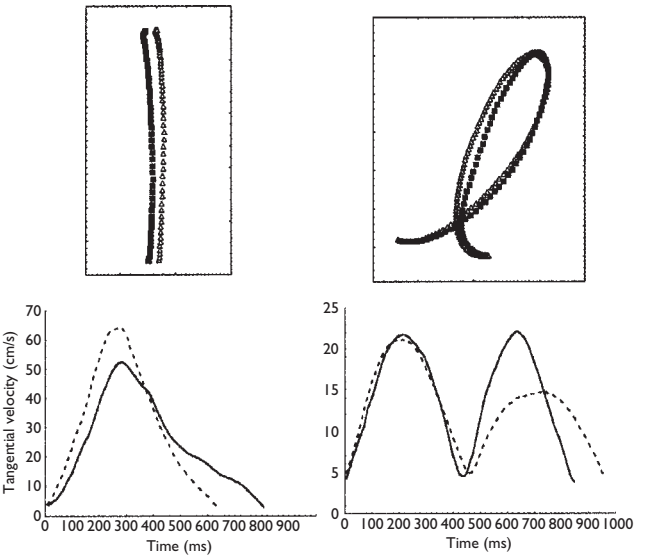

Fig. 1. Description of the stimuli used in the experiment. The first row shows the moving dot trajectory projected to the subject by the presentation software, and the second, the tangential velocity profile of the dot motion. In the pointing anticipation (PA) condition (left column), stimuli shows the first component of a representative pointing movement toward an intermediate 1.5 cm width target when the final target is large (top: triangle; bottom: dashed line) or small (square; solid line). The two trajectories are placed at different x values for sake of clarity. The reaching movement kinematics change with the size of the final target. In the writing anticipation (WA) condition (right column), stimuli shows the first component in the diagram 'ln' (triangle; dashed line) and in the diagram 'll' (filled square; solid line). The kinematics of the 'l' changes as a function of the following letter.

In the three conditions PA, WA and OM the presented stimuli only depicted the first sequence of a movement, i.e. the first pointing to the intermediate target and the first letter 'l' of the couple, both indicated in Fig. 1, and the movement of the ball before bouncing on the cushion, respectively. Thus the presented kinematics ended shortly before the finger reached the intermediate target in PA, shortly before writing of the first letter ended in WA and shortly before the ball bounced in OM. Subjects were then asked to anticipate the goal of the whole sequence, either reaching a large or a small target for PA, writing 'll' or 'ln' for WA, or the object going near or far for OM, in a forced-choice paradigm. In the baseline condition, participants had to answer up or down. In each condition, the participants were encouraged to answer quickly on the basis of their first impression by pressing on the corresponding button on the screen using a mouse. A short (900 ms) interstimulus interval elapsed before the next stimulus began.

PET measurements: Each condition was presented three times, and consisted of 22 trials, half for each alternative,

in a randomized order. The order of scan condition was randomized within each subject. Each condition lasted about 75 s, and task presentation started 15 s before the radioactive tracer reached the brain. Ten minutes elapsed between each injection. Thus, 12 PET scans per subject were recorded using a Siemens CTI HR+ (63 slices, 15.2 cm axial field of view) PET tomograph. A total of 63 transaxial images with a slice thickness of 2.42 mm without gap were acquired simultaneously. Emission scans were attenuation corrected with a transmission scan collected before the experiment. After a 9 mCi bolus injection of $H_2{}^{15}O$, scanning was started when the brain radioactive count rates reached a threshold value and continued for 45 s. Integrated radioactivity accumulated in the scanning was used as an index of rCBF.

Image analysis was performed on Silicon Graphics stations using statistical parametric mapping (SPM99 software Wellcome Department of Cognitive Neurology, UK) [19]. The scans of each subject were realigned, transformed into a standard stereotaxic space using a reference template image, and smoothed with an isotropic Gaussian filter of 12 mm full-width at half-maximum. The voxel dimensions of each reconstructed scan was $2 \times 2 \times 4$ mm in the x, y and z dimension, respectively. Simple comparisons were made using t statistics and converted into Z scores. All contrasts were thresholded at $p < 0.0005$ uncorrected for multiple comparisons.

As contrasts between conditions of interest (PA, WA, OM) and baseline (BA) yielded several similar activation foci, a masking procedure included in SPM was used to differentiate clusters activated in all contrasts and clusters specific to one contrast. Exclusive masking eliminated voxels that were significantly activated in the contrast describing the activation related to mechanical object motion (OM-BA) at $p < 0.005$ when calculating the two contrasts of interest related to human movement (PA-BA and WA-BA).

The activation foci were superimposed on a reference MRI, and anatomical identification was performed with reference to the atlas of Duvernoy [20]. Condition-specific parameter estimates, which reflect the adjusted rCBF relative to the fitted mean and expressed as a percentage of whole brain mean blood flow were calculated in the regions of interest.

RESULTS

Behavioral results: Participants were skeptical as to their ability to discriminate between the pair of events in the human motion condition during the PET sessions. Their behavioral responses show that their predictions were greater than chance level in the pointing and writing anticipation conditions ($77 \pm 21\%$ and $83 \pm 14\%$ of correct answers respectively), as well as in the object motion anticipation ($86 \pm 7\%$). This demonstrates their ability to anticipate the likely continuation of the events and their engagement in the different tasks during the cerebral blood flow measurement.

Neuroimaging results: Contrasts between the three conditions including motion (WA, PA, OM) and the baseline (BA) were computed to isolate activation related to the anticipation procedures. The three computed contrasts yielded similar areas of activity, in particular in the frontal lobe. Since the interest lied in isolating areas specific to the anticipation of stimuli linked to human action (either pointing, condition PA, or writing, condition WA), the contrast describing nonbiological anticipation, OM-BA, was used as an exclusive mask for the contrast describing human motion anticipation contrasts, PA-BA and WA-BA. Results for the contrast OM-BA are given in Table 1, and show mainly clusters of activity in the anterior part of the right hemisphere, i.e. in the prefrontal, orbital and insular cortices. Asterisks indicate clusters also found in the two simple effects of interest.

The results of the perceptual anticipation in the writing and pointing conditions, given in Table 2, show clusters common to the two contrasts in the left inferior frontal and orbitofrontal cortices, and clusters specific to each of the contrasts. The cortical areas of interest given the neural simulation hypothesis, i.e. the left pars opercularis and superior parietal lobule (SPL) in writing anticipation and the left premotor cortex and right intraparietal sulcus (IPS) in pointing anticipation, were subsequently analyzed using parameter estimates (Fig. 2).

A third set of contrasts between pointing and writing anticipation on the one hand and object anticipation on the other hand was computed (Table 3) in order to assess brain areas involved in the perception of the different stimuli notwithstanding the anticipation task. As in the previous comparison, results indicate common and different activation foci, in the left superior parietal lobule, intraparietal sulcus and inferior temporal gyrus, and in the left pars opercularis and inferior temporal gyrus for writing anticipation and left lateral orbital gyrus for pointing anticipation, respectively.

DISCUSSION

Although the human capacity to anticipate forthcoming events when observing someone else's actions has clearly been demonstrated by numerous psychophysical experiments, the neurofunctional basis of this capacity is still discussed. A privileged theoretical explanation involves simulation, i.e. representing the mental activities and processes of others by generating similar activities and processes in oneself [21]. In a neurofunctional perspective of this theory, one would expect anticipation of visual events to activate the same areas that have been found to

Table 1. Regions of increased brain activity associated with the simple effect OM-BA.

Region	Z score	Coordinates		
		x	y	z
Right superior frontal gyrus	4.00	28	26	60
SMA proper	4.31	−6	14	48
Right middle frontal gyrus*	4.00	50	38	26
Right lateral orbital gyrus*	5.87	40	56	2
Right insula*	4.33	42	22	−6
Right medial orbital gyrus*	4.83	22	54	−16

Voxel threshold 15, $p < 0.0005$. Asterisks denote clusters found in the two other simple effects at the same threshold. Coordinates are given in the MNI stereotaxic space.

Table 2. Regions of increased brain activity associated with the contrasts WA-BA and PA-BA masked exclusively with the simple effect OM-BA at $p < 0.005$.

Region	Writing anticipation		Pointing anticipation	
	Z score	Coordinates	Z score	Coordinates
Left inferior frontal area	4.85	−42,28,18	3.77	−44,28,18
Left lateral orbitofrontal	4.61	−46,46,−6	4.25	−46,44,−12
Left superior parietal lobule	3.60	−26,−74,46		
Left pars opercularis	4.41	−40,18,20		
Left hippocampus	4.09	−28,−12,−22		
Right intraparietal sulcus			3.82	38,−58,66
Left premotor area			3.79	−22,10,44
Right dorsolateral thalamic nuclei			3.84	8,−12,14
Right posterior orbital gyrus			4.00	40,26,−16

Voxel threshold 15, $p < 0.0005$. Coordinates as in Table 1.

be specifically activated when actually performing the motor actions. In this study, this motor-related activity should be restricted to the conditions in which anticipation is tackled by human motion, namely pointing and writing anticipation. Therefore, the control contrast (OM-BA; Table 1) used for masking reveals the brain network implied in anticipation in a broader sense, i.e. predicting the forthcoming event in a sequence notwithstanding its nature. This contrast shows several clusters in the right frontal and the orbitofrontal regions, most of them also revealed by the two other simple effects (PA-BA and WA-BA; data not shown). This result demonstrates that all contrasts involving anticipation imply a similar neural mechanism. The orbitofrontal foci can be explained by the fact that in the control condition OM, as well as the conditions of interest WA and PA, and not in the baseline BA, the right answer was unknown to the subject so that he had to make a prediction about this result. Indeed, activation in the orbital areas has been related with neuroimaging [16] to reward expectancy, in particular when there is an ambiguity in the answer. Therefore, similar processes of expectancy in WA, PA and OM could account for the commonality of the orbitofrontal activated clusters.

The dorsolateral prefrontal cortex (DLPFC) is engaged in cognitive processing and working memory [15], and was only found in the contrast describing object anticipation, OM-BA. Object anticipation can then be considered as a high-level cognitive task, whereas the two others, PA and WA, cannot. Anticipation from biological motion not being a high-level cognitive task reinforces the neural simulation hypothesis.

Since conditions PA, WA, and OM all contain an anticipation task, contrasts between these conditions, such as those described in Table 3, should remove areas com-

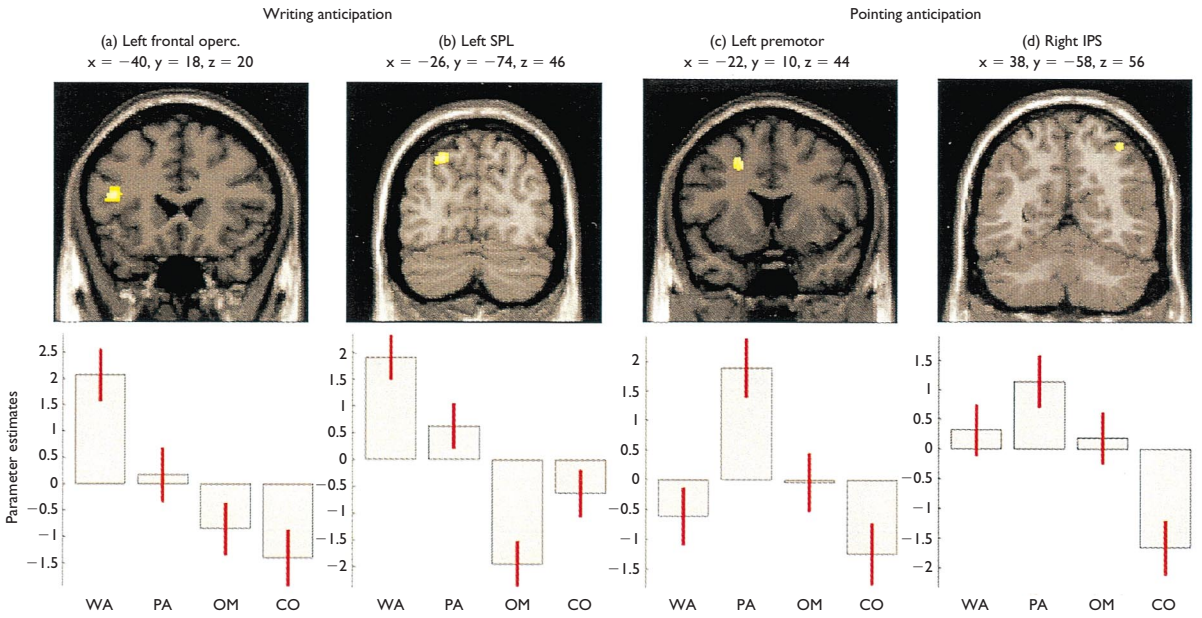

Fig. 2. Parameter estimates of the activity in the left frontal operculum (**a**) and superior parietal lobule (SPL; **b**) found in writing anticipation and in the left premotor cortex (**c**) and right intraparietal sulcus (**d**) in pointing anticipation. The first row shows coronal sections of a standard brain with the superimposed activated foci. The second row gives the parameter estimate of the corresponding cluster. Coordinates as in Table 1.

Table 3. Regions of increased brain activity associated with the contrasts WA-OM and PA-OM.

Region	Writing stimuli		Pointing stimuli	
	Z score	Coordinates	Z score	Coordinates
Left superior parietal lobule	6.12	−26,−74,44	3.94	−26,−74,44
Left intraparietal sulcus	3.76	−28,−62,30	3.99	−30,−62,28
Right inferior temporal gyrus	3.89	68,−50,−12	4.41	66,−48,−12
Left pars opercularis	3.67	−40,22,16		
Left inferior temporal gyrus	4.39	−56,−60,−12		
Left lateral orbital gyrus			4.02	−44,44,−18

Voxel threshold 15, $p < 0.0005$. Coordinates as in Table 1.

monly activated by this task. These results therefore indicate areas related to the processing of the stimuli, i.e. observing a writing or a pointing movement. Interestingly, both stimuli activate similar clusters in the left parietal cortex, already acknowledged to be involved in action observation [12]. Moreover, the WA-OM contrast also shows activation in pars opercularis, that will be discussed hereafter. This implies that this activity could be elicited by perception independently of the task.

The main result from this study concerns cortical areas specifically activated in the two tasks of interest as isolated with the masking procedure described in the result section (Table 2). Two foci, in the left orbitofrontal and in the inferior frontal cortices, were found in the contrasts describing the effects of WA and PA. These foci could be related to the perception of biological or human features. Aside from these areas, each contrast yielded specific foci. The left pars opercularis (Broca's area) and the left superior parietal lobule (SPL; see also Table 3) were activated for the writing anticipation, and the left premotor area and the right intraparietal sulcus (IPS) for the pointing anticipation (Fig. 2). Results for the two tasks involving anticipation from human motion involve fronto-parietal circuits, which are fundamental elements in the control of action in the monkey and, putatively, in humans [22]. The observed pattern of activity is therefore coherent with an involvement of the motor system in the tasks of interest.

Our results show that pointing anticipation specifically activates the right IPS and the left premotor area. Functional anatomy of pointing movements has been extensively studied with neuroimaging. In short, results have shown the involvement of the left premotor cortex in the preparation of action and the superior parietal region around the IPS in the visual control (e.g. [17] and references therein). Moreover, regions of the premotor cortex and the IPS are both functionally and anatomically connected in the monkey [22].

The lateralization of the IPS activation in the non-dominant hemisphere is an intriguing finding which could be explained by taking into account a recent study of the differential neural activity when acting in near versus far space in normal subjects [23]. Foci of activity were exclusively in the left dominant hemisphere when subjects acted in near space, and predominantly in the right hemisphere when acting in the far space. Thus, the right IPS activity found in our study could imply that the movement depicted by the stimuli were considered as being far in the subjects perspective. The right IPS and left premotor were not found when PA was contrasted with OM, so that activation in these two areas is congruent with the hypothesis that subjects used their own pointing production system when asked to anticipate the answer in the pointing anticipation task (see Fig. 2).

Broca's area role in the production of language, an old result from aphasic patients, has been confirmed using neuroimaging. For example, Binder *et al*. [18] interpreted Broca's role as a language executive, i.e. a region involved in the control of language-related tasks in a broad sense. It is interesting to note that Wernicke's area, believed to be specifically involved in the auditory aspects of language, was not activated in this experiment. On the other hand, cases of pure agraphia have been associated with lesions of the left superior parietal lobule [24] (but see also [9]), and this area have been activated in an fMRI study on the neural substrates for writing [25]. The left superior parietal cortex is postulated to be (one of) the center(s) for the kinematics of writing. This would imply that our Writing Anticipation task exclusively tackles areas linked to the written form of language, i.e. Broca's area and the left superior parietal lobule.

CONCLUSION

At a covert level, since subjects were unaware of their performances, anticipating the following motor event when observing someone activates brain areas involved when actually preparing and performing the same action. Our study provides neurophysiological ground to the psychophysical data that suggest that visual perception of human motion is partly dependent on the motor capacities of the observer [4]. Using our own motor capacities to understand the actions performed by others is at the core of the simulation theory [21]. Our results therefore strongly support the hypothesis that the neural motor system involved in the preparation and execution of action, is also part of a simulation network which is used to interpret the perceived actions performed by others [14,21]

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