The neural correlates of Fitts's law in action observation: An fMRI study

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Previous neuroimaging studies support the assumption of a strong link between perception and action, demonstrating that the motor system is involved when others' actions are observed. One question that is still open to debate is which aspects of observed actions engage the motor system. The present study tested whether motor activation corresponds to the difficulty of the observed action, using Fitts's law. This law postulates that the difficulty of any movement (ID) is a function of the distance to the target (A) and the target width (W). In an observation task, the ID of the observed action was manipulated orthogonally to W (by using five different As). The results revealed activity in the primary motor cortex, the supplementary motor area, and the basal ganglia in response to increasing ID levels, but not in response to different levels of A or W. Thus, activation in the motor system during action observation is not driven by perceptual parameters but by the motor difficulty of the observed action.

Numerous studies have shown that the motor system participates in action observation (e.g., Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2006; Grèzes & Decety, 2001; Hamilton & Grafton, 2007; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). For instance, it is known that people can acquire new motor skills through observation (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Mattar & Gribble, 2005) or mental imagery that entails mentally rehearsing actions (Olsson, Jonsson, Larsson, & Nyberg, 2008). Furthermore, acquiring new motor skills influences the way people observe others' actions that require the same skills (Aglioti, Cesari, Romani, & Urgesi, 2008). Similarly, behavioral studies on motor laws, such as Fitts's law (Fitts, 1954), suggest that motor laws constrain action production and action simulation in the same way (Grosjean, Shiffrar, & Knoblich, 2007; Decety & Jeannerod, 1995). In particular, both

the speed with which an action can be performed and the speed at which an action is perceived as being just doable are governed by the index of difficulty as formulated by Fitts's law. Thus, the same speed–accuracy trade-off observed in human performance dictates people's judgments about what is doable for others.

Briefly, Fitts's law parameterizes this trade-off characterizing biological motion. Accordingly, the average movement time (MT) to reach a target is defined as a linear function of index of difficulty (ID) of the movement:

$$MT = a + b \times ID$$

ID in turn is a function of the distance to be covered, commonly referred to as amplitude (A) and the width (W) of the target to be reached:

$$ID = \log_2(2A/W)$$

The longer the distance to the target, the more difficult the action becomes. By the same token, increasing target width reduces the accuracy requirement of the action and thus the index of difficulty. Fitts's law holds for most performed actions (with the notable exception of saccadic eye movements—Chi & Lin 1997; see also Danion, Duarte, & Grosjean, 1999), as well as imagined (Decety & Jeannerod, 1995) and perceived actions (Eskenazi, Grosjean, Humphreys, & Knoblich, 2009; Grosjean et al., 2007).

The study conducted by Grosjean and colleagues (2007) presented participants with alternating pictures of a person moving an arm between two identical targets, and they were asked to judge whether an average person could perform the observed movement at this speed. ID was systematically varied, choosing appropriate target widths and movement amplitudes. In other words, motor difficulty was varied so that it could not be derived from perceptual information about movement amplitude or target size alone. Rather, it reflected the difficulty of performing the observed movement. The results clearly showed that ID was an excellent predictor of the participants' "doability" judgments, providing strong support for the notion that motor constraints can influence perception (Grosjean et al., 2007).

The above findings provide evidence that motor simulations (Jeannerod, 2001; Wilson & Knoblich, 2005) are a ksey mechanism through which the motor system contributes to observation of actions. Motor simulation, in the context of action perception, refers to applying internal models that are used in planning and execution of one's own actions to perceived actions. Evidence for the involvement of motor-related brain regions during action perception is further provided by numerous neuroimaging studies (for a recent review, see Rizzolatti & Sinigaglia, 2010). Neural areas famously comprising the human mirror system, also known as the action observation network (AON) (Grafton, 2009), include the bilateral superior temporal sulcus (STS), the inferior parietal lobule (IPL), the inferior frontal gyrus (IFG), and the premotor cortex (PM). Other neural regions outside this mirroring network contributing to motor production, such as the supplementary motor area (SMA) (Dayan et al., 2007; Hamilton & Grafton, 2007), the basal ganglia (BG) and cerebellum (Blakemore, Frith, & Wolpert, 2001; Wolpert, Miall, & Kawato, 1998), and, importantly, the primary motor cortex (M1) (Caetano, Jousmaki, & Hari, 2007; Kilner & Frith, 2007; Kilner, Marchant, & Frith, 2009), have also been implicated in action simulation.

The mirroring system in humans is thought to support action understanding by recognizing actions in terms of their general aspects, particularly their object-related goals (cf. Rizzolatti & Sinigaglia, 2010), or the intentions delineated by the context in which the action is embedded (Iacoboni, 2005). This has been further elaborated by other theories of action perception. For example, it is argued that recognition is realized at several levels of visual-motor hierarchy in the human brain, each of which is encoded by a different node of the action observation network (Grafton, 2009; Hamilton & Grafton, 2008). These levels include the long-term goal or the intention level, the goal level, and the muscle/kinematic level of action representation. The short-term, object-related goal of an action is encoded in the anterior IPL, whereas the kinematics of primarily grasping actions is represented in the IFG node, an area hypothesized to support representation of produced movements.

There is also evidence that motor simulation taps into more specific parameters of observed movement as well, such as effort, speed (Aglioti et al., 2008), force (Slifkin, 2008; Wolpert & Flanagan, 2001), or internal states derived from the kinematics (Bosbach, Cole, Prinz, & Knoblich, 2005). Studies of peripheral activity during observation of effortful actions provide a similar picture. Increase in autonomic responses such as respiration and heart rate are reported during simulation of (Mulder, de Vries, & Zijlstra, 2005) as well as observation of effortful tasks (Decety, Jeannerod, Durozard, & Baverel, 1993). It has also been shown that participants have an accurate judgment of task difficulty prior to execution. This finding clearly suggests that motor simulation is the mechanism through which a judgment is reached (Frak, Paulignan, & Jeannerod, 2001). Witt, Proffitt, and Epstein (2005) demonstrated that people perceive the effort involved in an anticipated task in terms of their action capabilities. Of particular interest, perceived difficulty at a Fitts's task has been shown to correlate with the actual index of difficulty of the task (Delignières, 1998).

It is unknown whether or how the motor-related brain areas are involved in simulating the specifics of an action, particularly the difficulty as formulated by Fitts's law (Fitts, 1954). To investigate this question, we conducted a functional magnetic resonance imaging (fMRI) study of action observation, with a paradigm similar to the one described in Grosjean et al. (2007). In this paradigm, participants were asked to judge the "doability" of perceived actions. In the present study, participants viewed a pointing human hand alternately moving between two targets of identical size. Three different levels of ID were obtained with different combinations of target width
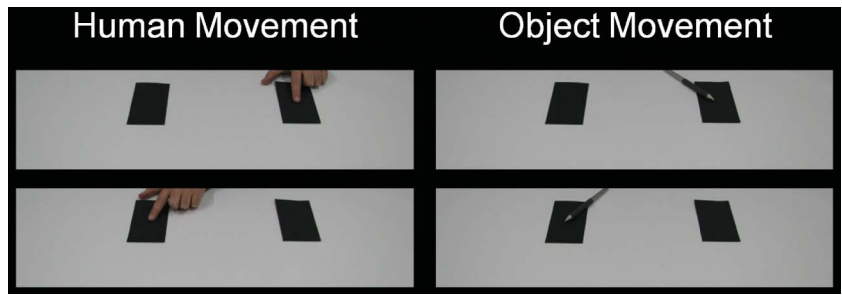
Figure 1.   Stimuli examples for ID2-W8 combination. Left panel: human movement as depicted by a hand moving between two identical targets. Right panel: object movement depicted by a pen moving between two identical targets.

(W) and distance (A). In accordance with the simulation account, we predicted increasing activity in motor areas with increasing levels of ID. We hypothesized that observed ID, which is a function of these two variables, but not object information (i.e., target width) or the contextual setup of the observed movement (i.e., distance between targets, movement amplitude), would activate the motor system of the observer. We did not expect to find a similar motor activation in a control condition, in which a pen instead of a pointing hand moved between the two targets (Figure 1). We predicted that, despite the perceptual similarity between hand and object stimuli, the motor system would be activated only during human movement and not during object movement.

METHODS

Participants

Ten right-handed participants (age range 20–29 years, six women) were paid to take part in the experiment. All gave their informed consent and were naive to the purpose of the experiment. None had a history of any neurological or psychiatric disorders, and their vision was normal or corrected-to-normal. Data from one participant were excluded from analysis due to an incidental lesion discovered in his right hemisphere. He was referred to a medical professional. The study was approved by the local ethics committee.

Behavioral task

Stimuli and procedure

Prior to the scanning session, participants were asked to perform the behavioral task described in Grosjean et al. (2007). In this apparent motion paradigm, participants were presented with alternating still frames of a pointing finger that moved at various speeds between two rectangular targets. The task was to judge whether the person could perform the movement at the observed speed without missing the targets. Pairs of photographs depicted a right index finger touching one of two targets. Targets in each frame were of identical width (W) and were separated by a given distance (A). Three ID levels (2, 3, and 4) were factorially crossed with three W levels (2, 4, and 8 cm), resulting in five As (Table 1). The frames were alternated at varying rates—-stimulus-onset asynchrony (SOA)—-that ranged from 120 to 720 ms with 40-ms increments. The experiment consisted of three blocks, with 144 trials randomly presented in each block. A MacBook Pro Macintosh computer running PsyScope (Cohen, MacWhinney, Flatt, & Provost, 1993) was used for stimulus presentation and response collection.

Data analysis

For each participant, the proportion of "possible" judgments was computed for each of 144 W $\times$ ID $\times$ SOA combinations. Then, for each of the 9 W $\times$ ID combinations, the perceived MT was defined as the SOA at which the participants gave an equal proportion of possible and impossible judgments (for details concerning this analysis, see supplementary materials). To test whether the data obeyed Fitts's law, linear regression analyses on the perceived MTs were performed with either ID or movement amplitude as

TABLE 1
Movement amplitudes (in cm) used in the experiment as a function of the target width and index of difficulty

Target width (cm)	Index of difficulty		
	2	3	4
2	4	8	16
4	8	16	32
8	16	32	64

the predictor variable. The analyses were carried out with MATLAB (The Math Works Inc, MU Guide - Inc., Natick, MA, 1998).

fMRI task

Stimuli and procedure

A similar apparent motion paradigm was used in the task performed during fMRI data acquisition, albeit with a new set of stimuli. The participants observed a hand moving between two targets. In 20% of the trials, the participants were asked to provide a speed rating of the movement. As in the behavioral task, each of the photograph pairs depicted a finger or a pen (Figure 1) pointing at one of the two identical rectangular targets. Here, we included photographs of left and right hands, in order to control for laterality effects in the brain activity. The three levels of ID were set against three levels of W, yielding nine different combinations (Table 1). In contrast to the behavioral task, the SOA, that is, the rate at which the still frames alternated, was constant across trials. This was done to control for a potential SOA confound on the ID manipulation. Therefore, any differences in perceived speed would be solely a product of the varying target widths and the distance between them. For example, a sequence with a 500-ms SOA and a low ID may be perceived as a very slow movement, whereas the same sequence with a high ID may be perceived as a faster but still doable movement. As a control, we included an object-movement condition in which a pen, instead of a human finger, appeared to jump between the same targets, separated by the same distances. In order to minimize the perceptual differences between the two conditions, photographs were cropped to include only the hand, without the arm, in the human-movement condition. The object-movement condition presented the pen at an angle to the targets similar to that of the hand in the human-movement condition. It should be noted that this paradigm is particularly suitable for studying Fitts's law in an fMRI setup, as it does not require an actual motor response, ensuring that the observed results cannot be due to motor production confounds or movement-related artifacts.

Each trial began with a blank screen (500 ms) followed by a fixation cross (1000 ms), after which the stimulus pair was presented (Figure 2). Each still frame remained on the screen for 500 ms, producing three different sequence durations, 2000, 3000, or 4000 ms for the 2-, 3-, or 4-cycle sequences respectively. Pilot data showed that 4 cycles were sufficient

to induce an apparent motion. The length of the trials varied to facilitate the estimation of the HRF response per trial and also to ensure that events did not alternate at a fixed frequency, as the latter are usually associated with noise. The participants' task was to estimate the relative speed of the movement: (1) very slow, (2) slow, (3) fast, and (4) very fast. To prevent stimulation of the motor regions by response requirements, the participants did not respond in 80% of the trials. In the remaining 20% of trials, a question appeared on the screen following the stimuli pair, asking the participants to rate the speed of the observed motion by using the button box placed inside the scanner. The participants could not tell while watching the movement whether the prompt question would follow. The participants had a maximum of 4000 ms to respond to the question, and as soon as a response was collected, the next trial commenced. These randomly presented "catch" trials were included to ascertain participants' attention and were modeled separately in the data analysis.

The experiment consisted of 450 trials (= 3 ID × 3 W × 2 movement type, left-hand/right-hand OR object, repeated 25 times), presented in random order. To provide opportunities for pauses, the experiment was run in six blocks with 75 trials. Each block lasted for approximately 6 min. In order to increase efficiency, no null events were included in this experiment, as our main interest was to identify neural modulations in response to changes in ID (i.e., differences between conditions, rather than differences between a condition and a baseline). To present the stimuli and register event times, we used E-Prime (Psychology Software Tools, Pittsburgh, PA, USA).

fMRI data acquisition

We used a Philips 3T Achieva system (Philips Medical Systems, Best, The Netherlands) to acquire blood-oxygen-level-dependent (BOLD) contrast-weighted echo-planar (EPI) for the functional scans. We acquired 38 slices, 2-mm-thick, with a 1.25-mm gap, resulting in an in-plane resolution of 2 × 2 mm, with an 80° flip angle, 35-ms echo time, and 2110-ms slice repetition time (TR). Images were acquired with an eight-channel phased array coil with a sense factor of 2. To minimize susceptibility artifacts, shimming was performed for each acquisition run, and the slices were tilted along the frontal-temporal cortex (Deichmann, Gottfried, Hutton, & Turner, 2003). The slices covered the entire brain, including the parietal cortex and the cerebellum.
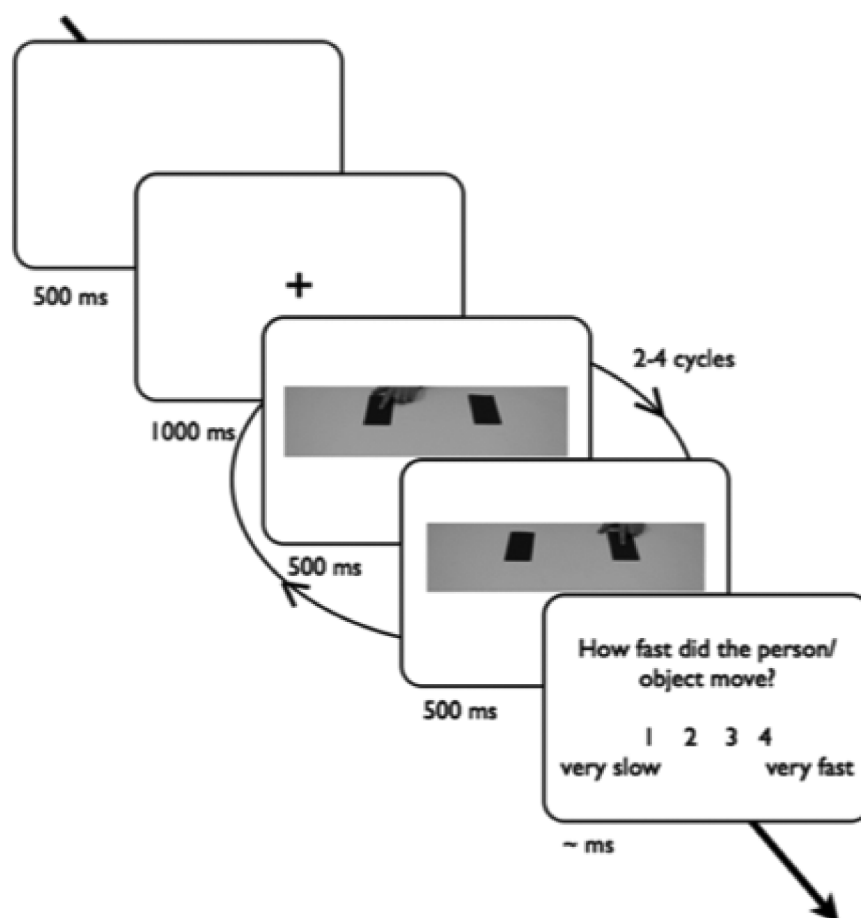
Figure 2. Example trial of the task presented in the scanner.

fMRI data analysis

Whole-brain, voxel-based analysis was done with SPM5 (Wellcome Department of Imaging Neuroscience, London, UK, www.fil.ion.ucl.ac.uk/spm). In preprocessing, the EPI volumes were first spatially realigned to correct for movement artifacts (Ashburner & Friston, 2003a) and motion by distortion interactions (Andersson, Hutton, Ashburner, Turner, & Friston, 2001). The volumes were then transformed to the Montreal Neurological Institute (MNI) standard space (Ashburner & Friston, 2003b) and smoothed with a 9-mm Gaussian kernel to account for residual intersubject differences and to accommodate assumptions of random field theory used for family-wise error corrections (Worsley & Friston, 1995).

Linear effects of ID change

First-level analysis consisted of modeling single-subject BOLD responses in a design matrix that included the onset and duration of stimulus pairs for 18 conditions (3 IDs $\times$ 3 Ws $\times$ 2 movement condition). Note that the A values (the distance between two targets) are determined by W and ID. Therefore, these were not modeled directly. In order to ensure that motor output could not affect differences in brain activation across conditions, catch trials were modeled separately and not included in further analyses.

The regressors in both models were convolved with two basis functions: the canonical hemodynamic response function (Friston, Harrison, & Penny, 2003) and its derivative that captures fluctuations in response onset (Friston, Penny, & Glaser, 1998). To correct for signal changes due to residual head movement artifacts, the six realignment parameters were included in the design matrix. Low temporal fluctuation in the data was modeled with a set of harmonic vectors (high-pass filtering 1/128 Hz) likely to be associated with scanner and physiological noise (Josephs & Henson, 1999).

Linear contrasts pertaining to the effects of ID, W, A, and motion type were computed. For an

effect of increasing ID, we computed the following two contrasts per each subject: ID2 < ID3, ID3 < ID4. We also used the same technique for effects of increasing width—W2 < W4, W4 < W8—and for amplitude—A4 < A8 < A16 < A32 < A64 (the linear effect size of the covariates) (Table 1). The effect of movement type was computed by comparing responses during human movement to those during object movement.

To allow for inferences at population level, second-level analyses (separate for ID, W, A, and movement type) were computed with the contrast images created at the first level. A neural effect of increasing ID was tested by the conjunction (with global null: Friston et al., 2005) of ID2 < ID3 and ID3 < ID4. Note that the conjunction analyses used two orthogonal contrasts and ensured that we report only regions that showed an increased activation for ID at both levels (from ID2 to ID3 and ID3 to ID4). A similar conjunction analysis was performed for W (target width). It should be noted that these analyses did not assume any linear change. We also looked at the linear effect size for A (distance between targets). We report clusters, at $p < .001$ uncorrected, that were larger than 30 mm^3, unless otherwise specified (see supplementary materials). The entries represent the estimated response extracted from the first eigenvariate of a 6-mm^3 sphere centered on the maxima group response.

RESULTS

Behavioral data

Figure 3A depicts mean perceived movement time (MT) as a function of ID and W. As expected, ID was a significant predictor of perceived MT: $r^2 = .82$, perceived MT $= 72.1 + 53.6 \times$ ID, $F(1, 7) = 32.00$, $p < .001$. That is, mean perceived MT increased linearly with the ID of the observed movement. Figure 3B presents the same data plotted as a function of A instead of ID. As can be seen, A alone was not a good predictor of perceptual performance: $r^2 = .41$, perceived MT $= 194.4 + 1.8 \times$ A, $F(1, 7) = 4.93$, $p = .062$. These results replicate the findings of Grosjean et al. (2007) and are consistent with Fitts's law.

fMRI data

There were no above-threshold differential brain responses to left- and right-hand movements. Therefore, these two conditions were collapsed. Our
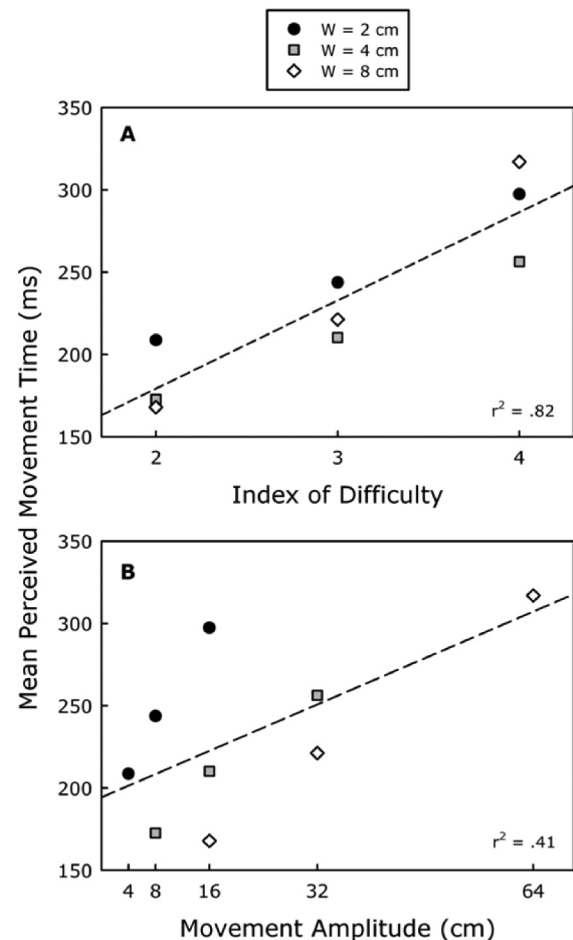

Figure 3. Mean perceived movement time as a function of target width (W) and (A) index of difficulty (upper panel) and (B) movement amplitude (lower panel). The corresponding linear regression lines and coefficients of determination are also provided.

main aim was to identify the neural structures that show a change in activity in response to an increase in ID, the main parameter of Fitts's law. We hypothesised that this information would be processed in structures known to be related to motor control. We predicted that these structures would show increased activation in response to an increase in ID of observed human movement, but not in response to an increase in W or A changes. To ensure that our results reflected a gradual increase of ID rather than being driven by the two extremes (i.e., ID2 vs. ID4), we used a conjunction analysis that tested for increases from ID2 to ID3 and ID3 to ID4. Results are reported with a mixed threshold approach with a peak height of Z > 3 and a cluster size ($p < .001$) of 30 mm^3 (Poline, Worsley, Evans, & Friston, 1997).

The results yielded increased activity in regions associated with motor execution and motor preparation, as ID of the perceived movement increased

TABLE 2
Conjunction analysis – human movement: ID2 < ID3 and ID3 < ID4

Anatomical labels		Min-t(8)	Cluster size	p value	Z		x, y, z (mm)	
Frontal								
SMA	R	2.73	421	.000	4.11	18	4	50
pCS	L	2.64	2076	.000	4.01	−40	8	42
CS	L	2.56	2076	.000	3.91	−48	−8	54
aCG	L	2.19	86	.000	3.45	−10	44	10
Superior orbital gyrus	L	2.49	339	.000	3.82	−16	20	−8
Subcortical								
Globus pallidus	R	2.62	184	.000	3.98	20	−2	12
Pons	L	2.35	147	.000	3.65	−6	−42	−28
SN	R	2.33	223	.000	3.62	10	−18	−24
Amygdala	R	2.6	366	.000	3.96	24	8	−22
Hippocampus	L	2.4	473	.000	3.71	−24	−14	−16
Occipital and temporal								
4th occipital	L	2.49	165	.000	3.82	−12	−82	−8
Calcarine	R	2.38	807	.000	3.69	10	−88	12
	L	2.34	196	.000	3.64	−18	−96	12
MTC	R	2.26	81	.000	3.54	50	−24	−14
aTP	L	2.4	473	.000	3.71	−40	−2	−26
	R	2.31	366	.000	3.6	50	0	−18

Notes: min-t(8) is size of the smallest of the effects from the two comparisons; SMA: supplementary motor area; pCS: precentral sulcus; CS: central sulcus; aCG: anterior cingulate gyrus, globus pallidus; SN: substantia nigra; MTC: middle temporal cortex; aTP: anterior temporal pole; L: left hemisphere; R: right hemisphere. We report clusters at $p < .001$, uncorrected, that were larger than 30 mm^3.

(Table 2 and Figure 4): central sulcus, SMA, precentral sulcus, and basal ganglia/globus pallidus (GP). In all these regions (Table 2), the correlation of BOLD responses to changing ID occurred only in the human-movement condition, and not in the object-movement condition. We note that at a cluster level, the effects for a change between ID2 < ID3 in the bilateral basal ganglia, left central sulcus, SMA, precentral sulcus, and GP survived family-wise error correction ($p < .05$; with voxel peak $p < .01$ and clusters extent > 500 voxels). Unfortunately, cluster-level corrections cannot be reliably applied to conjunction analysis (Friston, Holmes, Price, Buechel, & Worsley, 1999).

No effect of ID was observed in these regions for the object-movement condition ($p > .05$). This was tested by exclusive masking with the ID change for object-movement contrast. Furthermore, the activation in the CS, SMA, left precentral sulcus, and GP overlapped with regions that responded more strongly to human movement than to object movement, (tested by inclusive masking, $p < .05$). This provided further evidence that the neural structures involved in computing ID were also more likely to respond to human movements than object movements (Figure 5, also see supplementary materials). Importantly, activity in motor regions was observed despite the fact that participants were not executing any motor responses in these trials. There were no above-threshold activations that varied with ID in object-movement trials.

Further analyses showed that brain activation did not significantly increase in response to different amplitudes (A, $p > .01$, uncorrected) and different target size (W, $p > .01$, uncorrected). We also looked at the possible effects of decreasing ID (Winstein, Grafton, & Pohl, 1997). A similar conjunction analysis to that above was performed. However, this time, the contrast images were set up in the opposite direction (i.e., ID4 < ID3, ID3 < ID2). This analysis did not reveal any significant clusters at a threshold of $p > .01$, uncorrected. A weak effect of decreasing amplitude was observed, suggesting an increase in responses as the two targets were located closer to each other. This was observed in the left extrastriate cortex (BA 18, MNI: –18, –72, –2, Z = 3.43, $p < .001$, cluster = 30 mm^3), the left lateral orbitofrontal cortex (BA 47, MNI: –40, 50, –8, Z = 3.77, $p < .001$, cluster = 76 mm^3), and the medulla (MNI: –4, –18, –32, Z = 3.89, $p < .001$, cluster = 98 mm^3). This effect may potentially relate to visual crowding. Finally, there was no above-threshold response for decrease in target width (W, $p > .01$).

DISCUSSION

This study aimed to identify the neural structures sensitive to increasing difficulty (ID) of an observed action, as expressed by Fitts's law. The main finding
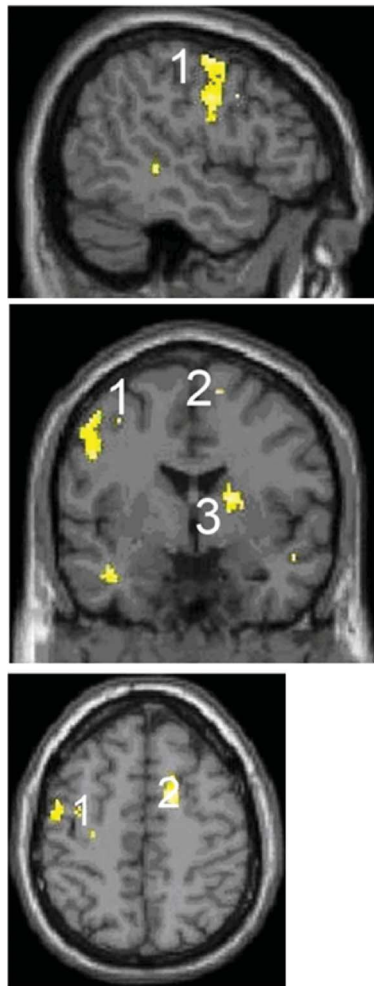
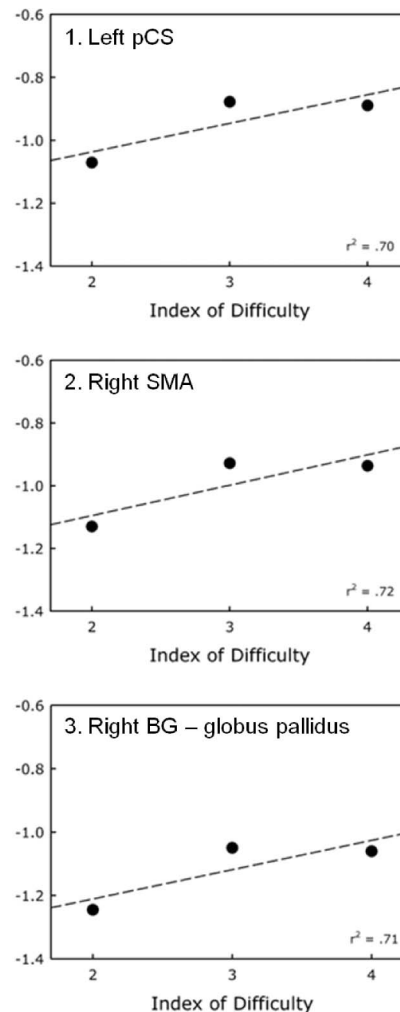**Figure 4.** Display of the conjunction SPM maps on a single-subject template T1: for human movement conditions, ID2 < ID3 and ID3 < ID4, at a combined threshold of maxima ($Z > 3$) and cluster ($p < .001$) larger than 30 mm^3. Areas that are sensitive to increasing ID are 1. left central sulcus (–48, –8, 54), 2. right SMA (18, 4, 50), and 3. right globus pallidus (20, –2, 12). The scatter plots on the y-axis the relative effect size for that region per each condition (arbitrary units) and on the x-axis the index of difficulty (ID).

was that activity in motor areas varied in response to increasing ID. These areas included the primary motor cortex, the right supplementary motor area, and the GP. This finding is further supported by a repetition-suppression analysis: Activation in these areas was suppressed as the same ID was repeated in the subsequent trial. As predicted, this pattern of activity in the motor system was observed only in the human-hand condition and not in a moving-object condition (Figure 4), showing that it was essentially biological action that engaged the motor system (Urgesi, Moro, Candidi, & Aglioti, 2006; but cf. Grosjean et al.,

2007). We also found that neurons in the SMA, M1, and GP were sensitive to the repeated levels of ID, showing a diminished response when ID level was repeated compared to when it changed. Again, this effect was specific to the human-movement condition. Finally, the W (target width) or the A (movement amplitude) variables did not reveal any differential activations. It should be stressed that the task used here manipulates ID orthogonally to the perceptual differences across conditions. In other words, the same ID level could be achieved through different W and A combinations.
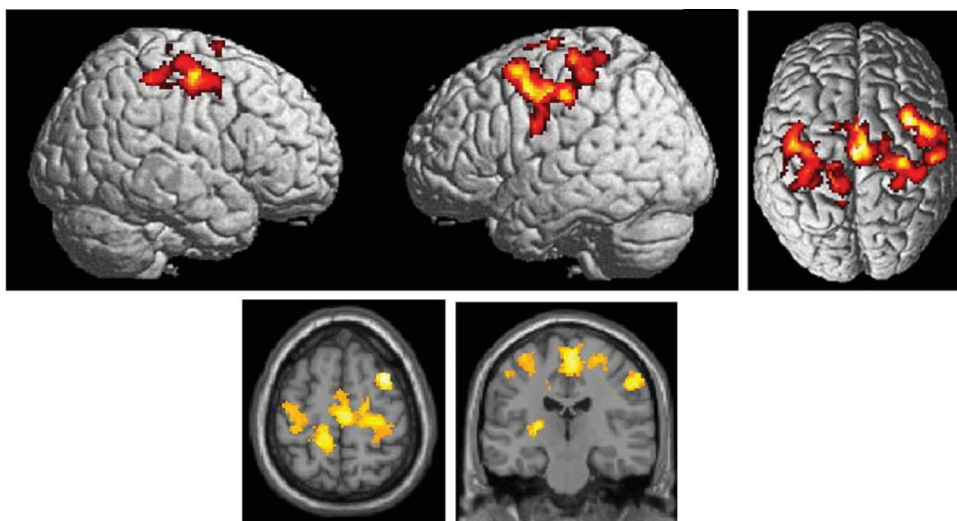
Figure 5. SPM maps for human movement > object movement contrast displayed on a rendered brain and on a single-subject template T1, at a combined threshold of maxima ($Z > 2.5$) and cluster ($p < .05$) larger than 200 mm³.

The brain areas that showed differential activation as a function of ID have also been shown to be involved in different types of action simulation, including motor imagery. Chiefly, the M1 is well known for its contribution to observation of actions (Grèzes & Decety, 2001; Munzert, Zentgraf, Stark, & Vaitl, 2008; Porro et al., 1996; Roth et al., 1996). The SMA, an area involved in simulation of motor sequences (Grafton, Arbib, Fadiga, & Rizzolatti, 1996), is a part of an overlapping network between motor imagery and action observation (Lotze, Laubis-Herrmann, Topka, Erb, & Grodd, 1999; Munzert et al., 2008; Zentgraf et al., 2005). The GP, a structure within the basal ganglia, has also been shown to be active during imagination and observation of movements (Gerardin et al., 2000; Munzert et al., 2008).

Surprisingly, we found no differences in cerebellar activity. The cerebellum has been implicated in internal models, specifically with respect to predictive timing in executed as well as simulated actions (Imamizu, 2000; Wolpert et al., 1998). This could perhaps be due to lack of speed differences in the observed movements. In order to avoid the confound of perceived speed, it was kept constant across different levels of IDs. Therefore, speed was always perfectly predictable, and this may explain why there were no differences in activation in the cerebellum. Thus, it is likely that the modulation of basal ganglia activation that was observed as a function of ID was also not due to differences in timing, although it is known that the basal ganglia play an important role in the timing of movements (Ivry & Spencer, 2004; Lewis & Miall, 2003). We have

recorded an activation increase in response to increasing levels of difficulty occurring in the right GP, a locus encompassing both internal and external GP (right GPi and GPe). Numerous neuroimaging studies, as well as lesion studies on neuropsychological patients (e.g., Parkinson's, Huntington's, and dystonic patients) show that these two nuclei of basal ganglia are important in regulating force control in produced actions (Aparicio, Diedrichsen, & Ivry, 2005; Prodoehl, Corcos, & Vaillancourt, 2009). More specifically, GPi activity has been found to parametrically scale with the rate of change in force production, and it has been suggested that the basal ganglia have a direct influence on hand representations of M1 (Prodoeh et al., 2009). Accordingly, the present results suggest that the observation of hand movements of varying difficulty scaled activation in a motor area that is specifically involved in hand force production.

It may seem surprising that the ID manipulation did not affect brain areas that have been described as the human mirror system (Rizzolatti & Sinigaglia, 2010). Whereas studies on mirroring in humans have demonstrated overlaps in neural activation between observed actions and corresponding motor representations in the observer, the present study manipulated a specific parameter of this match: the ID of the observed action. Thus, the differences in activity reflect how the motor system is modulated once a perception action match is established. Consistent with this reasoning, an early PET study that addressed the influence of ID on brain activation during task execution (Winstein, Grafton, & Pohl, 1997) found a similar pattern of neural activity as

the present study and no activation in the human mirror system.

The present results support the assumption that motor simulations are sensitive to motor parameters (ID) rather than perceptual parameters. The simulated difficulty of performing the action oneself (ID) rather than the perceptible differences in target size (W) or distance (A) drive motor system activation. Combining these results together with the lack of mirroring activity, one can speculate that human mirror circuitry was active throughout the experiment, thus allowing the motor system to run predictive forward models (Wilson & Knoblich, 2005) to simulate a particular motor parameter. The present findings might indicate that action perception is a complex process going beyond mere recognition of an action. Action perception seems to involve simulation of specific motor aspects of an observed action, and is supported by regions that extend beyond the human mirror circuitry.

In sum, the present study provides a neural basis for explaining previous findings where effort scales the perceived difficulty of observed or imagined actions (Delignières, 1998; Gopher & Braune, 1984) in different environmental conditions (Witt et al., 2004). To conclude, the present study adds to the body of converging evidence supporting tight links between perception and action. It provides clear evidence that the same constraints that govern motor performance during action execution also govern simulations in the motor system during action observation. Thus, when people observe others acting, they simulate the difficulty of the perceived actions by matching them to their own action repertoire. Whether this implies that we become exhausted when we observe others work hard remains to be explored.

AUTHOR NOTE

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