Neuronal encoding of human kinematic invariants during action observation

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Abstract

Human movements, besides entailing the presence of a body shape, comply with characteristic kinematic laws of motion. Psychophysical studies show that low-level motion perception is biased towards stimuli complying with these laws. However, the neuronal structures that are sensitive to the kinematic laws of observed bodily movements are still largely unknown. We investigated this issue by dissociating, by means of computer-generated characters, form and motion information during the observation of human movements. In a functional imaging experiment we compared the levels of BOLD activity elicited by human actions complying with or violating the kinematic laws of human movements. Actions complying with normal kinematic laws of motion differentially activated the left dorsal premotor and dorsolateral cortex as well as the medial frontal cortex. These findings suggest, that the kinematic laws of human movements specifically modulate the responses of neuronal circuits also involved in action recognition and that predominantly located in the left frontal lobe.

Introduction

The ability to perceive and understand the actions of others is among the most fundamental capabilities of the human brain, lying at the basis of social cognition. The high behavioral relevance of visual stimuli depicting the movements of conspecifics is underscored by several psychophysical studies showing specificities in their processing compared to other types of motion stimuli (Ahlström, Blake & Ahlström, 1997; Bertenthal & Pinto, 1994; Grossman & Blake, 1999; Neri, Morrone & Burr, 1998; Shiffrar & Freyd, 1990; Shiffrar, Lichtey & Chatterjee, 1997). During the past decades, many studies have sought to elucidate the neural mechanisms underlying these specificities. Many investigations, that used point-light displays as stimuli (Johansson, 1973) identified regions in the superior temporal sulcus, cerebellum, amygdala, premotor cortex, fusiform face area and lateral occipital complex that are sensitive to motion-defined bodily movements e.g. (Beauchamp *et al.*, 2003; Bonda, Petrides, Ostry & Evans, 1996; Grèzes *et al.*, 2001; Grossman *et al.*, 2000; Grossman & Blake, 2002; Peuskens *et al.*, 2005; Saygin *et al.*, 2004; Servos *et al.*, 2002; Vaina *et al.*, 2001). Further imaging studies that used videotaped sequences of human movements suggested that brain areas which are involved in planning, preparation and execution of movements are also activated during action observation (Buccino *et al.*, 2001; Decety *et al.*, 1994; Grafton, Arbib, Fadiga & Rizzolatti, 1996; Iacoboni *et al.*, 1999; Nishitani &

Hari, 2000; Rizzolatti *et al.*, 1996) (for a review see (Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004)). Finally, recent studies have also identified specific areas in the occipital cortex (Extrastriate Body Area, EBA; and Fusiform Body Area, FBA) that are selectively activated by static and dynamic displays depicting human bodies (Downing, Jiang, Shuman & Kanwisher, 2001; Peelen & Downing, 2005; Peelen, Wiggett & Downing, 2006).

Notably, human actions are characterized not only by the presence of a moving body, but also by the compliance of the performed movements with characteristic kinematic laws of motion. A well-established example is the so-called "two-thirds power law", that describes the characteristic dependency of the speed of human movements on the geometrical properties of the motion path. This empirical law states that when tracing a curvilinear path, the angular velocity A and the curvature C of the hand trajectory are related through an exponential law, i.e. $A=kC^{\beta}$, where $\beta\sim2/3$ and k is a piecewise constant coefficient called the velocity gain factor (Lacquaniti *et al.*, 1983). This law can be expressed in a mathematically equivalent manner in terms of the tangential velocity V, i.e. $V=kC^{\beta}$. In this formulation, which will be used here, a value of the exponent β equal to -1/3 gives precisely the two-thirds power law. The two-thirds power law is a ubiquitous feature of movement generation that characterizes drawing movements (Lacquaniti *et al.*, 1983; Viviani & Flash, 1995), eye movements (de'Sperati & Viviani, 1997), speech-related movements (Tasko & Westbury, 2004) and human locomotion along curved paths (Hicheur *et al.*, 2005). A notable characteristic of this law is that it holds not only in movement production but also in motion perception. Indeed, psychophysical and brain imaging studies with simple motion displays showed that human visual perception is biased towards stimuli complying with the two-thirds power law (Dayan *et al.*, 2007; Flach, Knoblich Günther & Prinz, 2004; Kandel *et al.*, 2000; Levit-Binnun, Schechtman & Flash, 2006; Viviani & Stucchi, 1992). This bias is a complex phenomenon whose mechanisms are still not fully understood. For example, a recent psychophysical experiment by Bidet-Ildei and colleagues found different behavioral performances in judging whether a visual stimulus complied or not with the two-thirds power law depending on whether the stimulus was a simple motion display or a point-light display depicting a person moving (Bidet-Ildei, Orliaguet, Sokolov & Pavlova, 2006).

The neuronal structures that are specifically sensitive to the characteristic kinematic laws of motion of the human body during action observation are still unknown. Previous neuroimaging investigations have contrasted the observation of natural as opposed to unnatural actions. e.g. by comparing human and robot movements (Gazzola *et al.*, 2007; Tai *et al.*, 2004) or biomechanically possible versus impossible movements (Costantini *et al.*, 2005; Stevens *et al.*, 2000). However, these manipulations affected human motion in a global manner and typically confounded changes of the kinematic characteristics of the movement with changes in the associated body shape or configuration. In particular, to our best knowledge, no brain imaging study in the literature has investigated, in a well controlled manner, how the neural substrates of the visual processing of bodily motion are influenced by those laws that reflect the underlying constraints governing human motor production (e.g. the two-thirds power law).

The goal of the present study is to investigate the neuronal substrates specifically subserving the visual processing of kinematic invariants during action observation while at the same carefully controlling for body shape cues across different conditions. A pre-requisite for achieving this goal is a set of stimuli in which body motion is controlled independently from body shape. Video-taped natural sequences cannot provide such a dissociation, since humans cannot produce movements that violate the two-thirds power law even after extensive training (Viviani, Campadelli & Mounoud, 1987). Thus, in order to achieve a complete control of form and motion features, we used methods from computer graphics. We used a professional rendering software package to animate a human-like avatar. Similar stimuli have been already used to investigate patterns of brain activity in response to well-controlled changes of high and low-level characteristics of human movements (Pelphrey *et al.*, 2003; Pelphrey, Morris & McCarthy, 2004). In our experiments we presented the subjects with a computer generated character that executed exactly the same movements, derived from motion captured data, but with different types of kinematic characteristics that either complied with or violated the two-thirds power law. In this way, the body shape of the avatar was kept constant across all conditions, and only the kinematics of the joint trajectories was changed. In a functional Magnetic Resonance Imaging (fMRI) experiment we then recorded and compared the Blood-Oxygen-Level Dependent (BOLD) responses of human subjects while observing movements that were either compatible or incompatible with normal kinematic laws of human movements.

Materials and Methods

Participants

Fourteen subjects (7 female and 7 male), age mean=26 and s.d.=3, participated in the experiment. All of them were right-handed and had normal or corrected-to-normal vision. Participants gave their written informed consent and were paid for their participation in the experiment. All the procedures were approved by the ethics committee of the University Clinic of Tübingen.

Visual Stimuli

Smooth curvilinear hand and arm movements of a human subject were recorded using a *Vicon 612* motion capture system (Vicon Motion Systems Ltd, Oxford, UK) with 7 cameras. The temporal sampling rate was 120Hz, and the spatial error was less than 1mm. The recorded movements were smooth, curvilinear and roughly resembled the three trigrams '*lll*', '*lle*' and '*leo*' written in the air with both hands. These movements were chosen since previous studies have shown that hand movements during the reproduction of these types of stimuli comply with the two-thirds power law (Kandel *et al.*, 2000). For the purpose of the experiment, we selected two repetitions of each of the three movements. The average duration of the movements was 2.61s±0.26s (see Table S1 in the Supplementary Materials).

Data were pre-processed using commercial software by *Vicon*. Movements were executed relatively slowly and most of the power was thus concentrated at low temporal frequencies. The power spectra plotted in Fig. S3 clearly show that frequencies above 2Hz contained only a negligible part of the power of the movement. Thus, similar to previous studies from other groups (Hicheur *et al.*, 2005; Schaal & Sternad, 2001), high frequency noise was removed by low-passing the recorded trajectories with a 5^{th} order Butterworth low-pass filter with a cut-off frequency of 3.6Hz.

For the recorded movements, the best power-law approximation of the relationship between the tangential velocity and curvature of the hands' trajectories yielded a value of -0.3±0.02, which is in agreement with previous results (Kandel *et al.*, 2000; Viviani & Flash, 1995) (see Figs. S1 and Tables S1 and S2 in the Supplementary Materials for a complete listing of the kinematic characteristics of the stimuli). Estimates of the exponent of the power law were largely insensitive to changes of the cut-off frequency up to a value of approximately 8Hz. In order to change the exponent of the power law by an amount Δ the tangential velocity V of each hand was multiplied by the factor C^{Δ}, where C represents the local curvature of the hand path. In this manner, the new power-law relating velocity and curvature was, on average, $V_{new} = kC^{\beta+\Delta}$. For the purpose of our experiment we set Δ=0.6, which yielded a final value of the exponent of 0.32±0.03. The value Δ=0.6 was selected based on pilot psychophysical experiments showing that such perturbation of the two-thirds power law yielded biological motion stimuli that were reported by the subjects as markedly unnatural (see Fig. S2). In order to ensure high spatial and temporal sampling, both the tangential velocity and the curvature of the left and right hand trajectories were computed from the polynomial coefficients obtained from the fitting of a cubic spline. The velocity profile V_{new} was integrated to obtain the temporal evolution of the hand's position. We then computed a time warping function that, when applied to the original movement, ensured that the new hand movement fulfilled the new kinematic profile. This computational step yielded two warping functions, one for each hand. Each of these warping functions was then applied to all the joints in the corresponding arm. The remaining points in the body not belonging to either arms, were characterized by very small movements and their trajectories were transformed using an average of the two warping functions. The characteristics of the hand trajectories before and after the perturbation of the kinematics for one of the six selected movements are shown in Fig. S1, whereas the kinematic characteristics for all the six movements are shown in Tables S1 and S2. Both the original and the "perturbed" stimuli had a sampling rate of 120Hz.

Stimuli with normal and perturbed kinematics were uniformly rescaled in time such that each stimulus lasted for 3s, were imported into a commercial software (3DStudio Max 9, Autodesk) and were used to animate a commercial avatar model. 3DStudio Max imports motion capturing data by first fitting them to a body model and then resampling them at a rate of 30 samples per second.

Two types of stimuli were created: '*normal*' stimuli in which the avatar moved following the original motion captured trajectories and '*perturbed*' stimuli in which the avatar moved following the time-warped trajectories. The faces of the avatar was masked with a gray ellipsoid in order to prevent additional activations of cerebral structures involved in the processing of faces. The scenes were then rendered in order to generate a set of 3s movies in AVI format (524 x 412 pixels at 30 frames/s) used for the experiments. An additional set of stimuli ('*static*') was created by extracting at regular time interval 6 snapshots from the "*lll*" animation.

Experimental design

During each scanning session, stimuli were displayed in 9s blocks, interleaved with 6s periods of fixation. Eight blocks were included for each of the three experimental conditions resulting in a total of 24 blocks. Each block contained either 3 successive animations belonging to only one of the two dynamic conditions (normal or perturbed) or 3 static posture images. The blocks were presented in a one-back counterbalanced manner. Each scanning session lasted a total of 390 seconds and was performed three times by each subject.

To control for eye-movements, subjects were instructed to carefully maintain fixation on a cross which was located at the center of the visual display throughout the entire session. Subjects were asked to perform a one-back task while watching the stimuli. When two identical stimuli (or static postures, in the static condition) appeared in succession, subjects were required to press a button in the response box. Instances of two consecutive identical stimuli were included in 50% of the blocks evenly distributed across the 3 conditions. Overall, subjects were able to perform the one-back task very well (97.6%, 95.2%, 97.6% for the '*normal*' '*perturbed*' and '*static*' conditions, respectively) and there were no significant differences among the three conditions with respect to this task (due to the violation of normality assumptions we used a Kruskall-Wallis test: $\chi^2=1.17$, $p=0.56$).

Stimulus delivery and response acquisition were controlled using the Psychophysics toolbox for MATLAB (Brainard, 1997; Pelli, 1997). Stimuli were projected with an LCD projector onto a tangent screen positioned behind the subject and viewed through a tilted mirror. Responses were collected with an MRI compatible response box.

Imaging Setup

The experiment was performed using a 3 Tesla Siemens TimTrio scanner (Siemens, Erlangen, Germany), equipped with a resonant gradient echo-planar imaging system. T2*-weighted functional images (TR=3s, TE=35ms) sensitive to the BOLD contrast were acquired in gradient echo-planar imaging (EPI) sequences. 44 slices (3mm height) were acquired for complete coverage of the cerebral and cerebellar cortex in descending order at 3x3x3 mm isotropic resolution (flip angle 90°, FOV 192 mm, image matrix 64x64). Anatomical scans used the 3D gradient-echo T1-weighted Siemens MPRAGE sequence (TI 1.1 s, TR 2.3 s, TE 2.92 ms) acquiring 176 slices in the sagittal plane at 1x1x1 mm isotropic resolution (flip angle 8°, FOV 256 mm, image matrix 256x256).

Data Analysis

Image pre-processing and statistical analysis were performed using SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). Functional image volumes were first unwarped and spatially realigned to the first image in the series to correct participants' head motion over time. Images were then corrected for slice timing differences by temporally interpolating the voxel time courses in each slice to align to the time of acquisition of the middle slice, spatially normalized and smoothed with a 8-mm Full Width Half Maximum (FWHM) isotropic Gaussian kernel. Structural T1-weighted images for each subject were also spatially normalized to the MNI space using the T1 template brain of SPM5.

Statistical analysis was based on the General Linear model (GLM) (Friston *et al.*, 1995) and consisted of two levels of analysis. At the first level, the time series of each voxel for each subject and experimental session were fitted with a design matrix, having a regressor for each of the three experimental conditions (normal, perturbed and static). The regressors were modeled as box-car functions convolved with the canonical hemodynamic response function. For each regressor, the baseline was defined by setting the value of the associated weights to zero. However, it is worth emphasizing that we obtained virtually identical results when the baseline condition was defined as the weights of the regressor modeling the fixation periods. At the second level, a random-effect GLM was applied on the individual parameter estimates obtained from the first-level analysis. Contrasts were thresholded at $p<0.001$ at the voxel level, and corrected for multiple comparisons, with a threshold of $p<0.05$, based on the spatial extent of the activated clusters. The method used for cluster size thresholding was that implemented in SPM5, which is based on Gaussian random field theory (Friston *et al.*, 1996; Friston *et al.*, 1994; Hayasaka & Nichols, 2003). Plotting of the contrasts of interest was performed by importing the results into MRICroN.

Eye Movements

In order to exclude the possibility that observed patterns of BOLD response during observation of 'normal' and 'perturbed' stimuli might be related to different oculomotor behavior in the two conditions we conducted a control experiment. The eye movements of four subjects were recorded monocularly using an MRI compatible pupilometry eye-tracking system (iView X MRI, SensoMotoric Instruments GmbH, Germany) inside the scanner under the same experimental conditions of the main experiment. Possible differences were assessed be means of t-test analysis on respectively the number and amplitude of saccades in the three conditions (n=normal, p=perturbed and s=static). No statistically significant difference was found in any of the pairwise comparisons across conditions both in the number (t_{np}=0,76, p_{np}=0.50; t_{ns}=-1,72, p_{ns}=0.18; t_{ps}=-1,56, p_{ps}=0.22) and amplitudes of saccades (t_{np}=-0,98, p_{np}=0,40; t_{ns}=-1,48, p_{ns}=0.24; t_{ps}=0.01, p_{ps}=0.99).

Results

In this study we investigated the neuronal correlates of the two-thirds power law during visual perception of human movements. For this purpose we compared BOLD responses of human subjects while observing computer generated human-like avatars performing curvilinear movements simultaneously with both hands in the air. Two main conditions were investigated (Fig. 1). In the first condition ('**normal**'), visual stimuli were rendered using the original hand trajectories derived from motion-captured data and thus the movements complied with the two-thirds power law. In the second condition ('**perturbed**') we time-warped the original trajectories in order to invert the normal relationship between the tangential velocity and the curvature (see *Materials and Methods* for details). That is, contrary to the normal behavior, the hands increased their velocity at points of high curvature and decreased their velocity at points of low curvature. It is worth emphasizing that the '*normal*' and '*perturbed*' stimulus classes differed only in the temporal characteristics of the movements whereas, the global spatial features of joint trajectories, and in particular the instantaneous joint configurations, were identical in the two cases. A third condition ('**static**') consisted of static snapshots extracted from the presented movies.

As shown in Fig. 2 and Table 1, two groups of areas in the frontal lobes exhibited significantly higher BOLD responses during observation of stimuli that were compatible with the two-thirds power law compared to stimuli that violated this motor invariant. The first group of areas was located in the left hemisphere and ranged from the dorsal part of premotor cortex (BA 6), extending frontally to the middle and frontal gyri (BA 8 and BA 9). The second focus of activity was located bilaterally, although with a stronger response in the left hemisphere, in the medial frontal cortex (BA 10, BA 32). Our analysis revealed no areas showing significantly increased activation for perturbed compared to normal stimuli. This result suggests the presence in the frontal lobe of a network of areas, mostly lateralized to the left hemisphere, exhibiting higher activity during observation of human movements complying with normal kinematic laws of motion.

A second analysis of both behavioral and brain imaging results was conducted in order to exclude that activation patterns in Fig. 2 might be, at least partially, related to motor responses. In our experimental paradigm subjects had to report, by pressing a button with the right hand, the occurrences of pairs of subsequent displayed identical stimuli. This simple 1-back task was included in order to keep the subjects' level of attention as constant as possible throughout the experiment. The occurrences of button presses were counterbalanced across conditions. However, a higher degree of activity of the left motor and pre-motor areas, possibly overlapping with foci of activity associated with the main contrast in Fig. 2, is expected in the case of significant differences across conditions in the number of button presses. This can be ruled out for two reasons. First, as reported in the *Materials and Methods* section, subjects' responses in the one-back task were monitored during scanning and no statistically significant difference was found across conditions. Second, in order to isolate the effect of button presses, we contrasted BOLD responses of sessions in which two subsequent identical stimuli occurred with those of sessions in which stimuli were all different. As shown in Fig. 3, button presses selectively activated regions in the left motor, supplementary motor and somatosensory cortex (BA 4, BA 3 and BA6) as well as the cerebellum and the insula. These areas are routinely activated during execution of hand movements (Buccino *et al.*, 2004; Rizzolatti *et al.*, 1996). Notably, all motor and pre-motor areas, activated in sessions containing button presses lay more posterior than activations found in the main experiment and activation patterns in the two cases were strongly separated. This result is in line with a recent suggestion by Picard and Strick (Picard & Strick, 2001) that the human dorsal pre-motor cortex can be divided into a caudal part (PMd proper), more involved in motor preparation and generation, and a rostral part (Pre-PMd) more involved in cognitive processes. In our experiment, areas in dorsal pre-motor cortex differentially responding during observation of movements complying with the two-thirds power law lay entirely within the Pre-PMd.

In a third analysis we sought to identify areas that were similarly activated during the observation of bodily movements independently of whether or not they complied with normal kinematic laws of motion. For this purpose we identified voxels that were common to the two contrasts "normal > baseline" and "perturbed > baseline". Results of this analysis are presented in Fig. 4 and show that the observation of a moving body, independently of its kinematics, produced a widespread pattern of activity. This pattern encompassed frontal, parietal and temporo-occipital regions that are typically activated during action observation and perception of biological motion (Beauchamp *et al.*, 2003; Grèzes & Decety, 2001; Grèzes *et al.*, 2001; Grossman *et al.*, 2000; Lestou *et al.*, 2008; Peuskens *et al.*, 2005; Servos *et al.*, 2002; Vaina *et al.*, 2001). Notably, it also included the superior temporal sulcus and regions in the inferior parietal lobe and in the inferior frontal gyrus, which are considered the putative human homologue of the monkey mirror neuron system (Buccino *et al.*, 2001; Iacoboni & Dapretto, 2006; Rizzolatti & Craighero, 2004). This result is in line with previous studies reporting activity in the mirror neuron system during observation of both human and robotic actions (Gazzola *et al.*, 2007) (but see (Tai *et al.*, 2004)) and possible vs. impossible movements (Costantini *et al.*, 2005; Stevens *et al.*, 2000). Furthermore, the widespread activation pattern reported in Fig. 4 was not caused by the one-back task. Indeed, very similar activations were obtained when activation patterns resulting from the two contrasts "normal > static" and "perturbed > static" were intersected (Fig. S5a). Since the one-back task was common to the "normal", "perturbed" and "static" conditions, the subtraction of this latter condition in the contrasts "normal > static" and "perturbed > static" discounts for its possible effects.

Discussion

We investigated the neuronal substrates subserving the processing of motor invariants during action observation. For this purpose we compared the BOLD responses of 14 subjects while observing human movements complying with or violating the two-thirds power law. We found that human movements complying with the two-thirds power law yielded higher levels of BOLD response in a network of structures encompassing the left dorsal pre-motor cortex, the middle and superior frontal gyri and medial frontal cortex. These results have implications for theories of action perception and are important for several reasons.

First, our results represent direct evidence that specific brain structures, mostly lateralized to the left hemisphere, exhibit significantly higher BOLD responses during observation of human movements complying with normal kinematic laws of motion. Our approach complements that of previous studies that investigated possible neuronal correlates of other characteristics of human movements. For example, Hamilton and Grafton reported that areas in the anterior intraparietal sulcus might represent the goal of observed action (Hamilton & Grafton, 2006), whereas areas in the inferior frontal cortex might more involved in coding the action outcome (Hamilton & Grafton, 2008). In a similar fashion, Lestou et al. found that areas in frontal and parieto-temporal cortex are differential modulated by the physical and perceptual similarity respectively of observed actions (Lestou *et al.*, 2008). The picture emerging from these studies is that action observation elicits a higher level of BOLD responses in a widespread network of areas, with different areas encoding different characteristics of the observed action. The present study adds to this picture by providing the first clear evidence that the kinematic laws of observed movements are among the characteristics encoded in this network of areas.

Second, our results suggest a specific role of the left dorsal pre-motor cortex in the visual processing of the two-thirds power law during action observation. While several previous studies suggest the involvement of the left pre-motor cortex in the visual analysis of human movements, a specific function of its most dorsal part is suggested by two recent studies by Calvo-Merino et al. (Calvo-Merino *et al.*,

2006) and Tai et al. (Tai *et al.*, 2004). In these studies neuronal structures in the left dorsal pre-motor cortex were differentially activated by the observation of actions that were already in the observer's motor repertoire (Calvo-Merino *et al.*, 2006) or human goal-directed movements when contrasted with the same movements executed by a robot (Tai *et al.*, 2004). Robot movements differ from those of a human with respect to both the body shape features and the kinematic features of the action. Our study carefully matched the body shape of the moving agent across conditions and thus demonstrates that the left dorsal pre-motor cortex shows also a clear preference for kinematic invariants of human motor behavior. Thus, in agreement with previous studies, our results show that structures in the pre-motor cortex are also selectively activated during movement observation. They further suggest that this selective activation critically depends on the degree of compliance of observed movements with normal kinematic laws of human movements.

Third, our results show that, in addition to the left dorsal pre-motor cortex, large parts of the middle and superior frontal gyri (BA 6, BA 8 and BA 9) exhibited higher levels of BOLD response to movements complying with the two-thirds power law. Experimental evidence shows that these dorsolateral frontal areas contain high-level visuo-motor representations of actions. For example, they are activated by action observation and imitation (Buccino *et al.*, 2004; Decety *et al.*, 1997; Koski *et al.*, 2003), "free willed" (as opposed to cued) finger movements (Hyder *et al.*, 1997), motor learning (Jenkins *et al.*, 1994), action words related to arm movements (Hauk, Johnsrude & Pulvermüller, 2004) and attributing an action to others (as opposed to self) (Farrer & Frith, 2002). The results reported here suggest that kinematic laws of motion form an important component of the representations of actions in the prefrontal cortex, thus providing novel insights into their nature. There are two possible caveats to this conclusion. The first caveat is that areas BA 8 is known to contain the Frontal Eye Fields and thus at least some portion of activations in that area might be due to oculomotor behavior. A detailed analysis of the subjects' eye movements in the scanner evidenced no differences both in the number and amplitude of saccades across different conditions (see Materials and Methods). Since eye movement recordings were performed in separate sessions than actual scanning these results do not provide a completely conclusive evidence. However, they strongly suggest that activation patterns in our experiments cannot be explained simply by differences in oculomotor behavior across the different conditions. The second caveat to our conclusions is that areas in the dorsolateral pre-frontal cortex were also reported to be selectively activated by memory tasks (Blumenfeld & Ranganath, 2006) and in particular by verbal memory tasks (Petrides, Alivisatos, Meyer & Evans, 1993). Thus, it seems possible that the differential activity in these regions might be related to memory-specific differences in performing the one-back task and in particular to verbal memory effects given that the movements resembled trigrams. Two reasons make also this explanation unlikely. First, the occurrences of trials requiring feedback from the subjects were carefully counterbalanced across conditions. Second, a detailed analysis of the behavioral responses in the scanner revealed no statistically significant performance difference across conditions (see *Materials and Methods*). Although making it unlikely, this behavioral evidence does not completely rule out the possibility that the subjects adopted different working memory strategies, that is verbal vs. non-verbal, to perform the one-back task. However, this explanation would predict activation differences in areas known to be involved in language production (e.g. Broca's area) (see for example Chein & Fiez, 2001; Chein, Fissell, Jacobs & Fiez, 2002), and we failed to observe such differences.

An unexpected finding of our experiment is the selective activation of medial frontal regions during observations of human movements complying with the two-thirds power law. Although not routinely activated during action observation, the ventro-medial frontal cortex, albeit a little bit more ventral than in the present study, has been found to be selectively activated during observation of movements already in the observer's motor repertoire in comparison with unpracticed movements (Calvo-Merino *et al.*, 2005). Motivated by studies showing that ventro-medial frontal cortex is strongly activated by rewarding stimuli (O'Doherty *et al.*, 2003) and might contribute to social judgments (Decety & Chaminade, 2003), Calvo-Merino and co-workers hypothesized that its activation in the context of action perception might reflect a higher degree of either "*pleasantness*" or social engagement of the perceived movements (Calvo-Merino *et al.*, 2005). The experimental paradigm used in our study was not designed to specifically investigate this hypothesis. However, our results motivate further experiments in order to test the possible relationship between the perceived "*pleasantness*" of human movements or motion in general and their degree of compliance with the two-thirds power law.

Fourth, the comparison of present experiment with our previous study (Dayan *et al.*, 2007), suggest possible differences between the processing of biological motion displays and abstract motion stimuli during visual perception of the two-thirds power law. In that study we compared the BOLD responses during observation of a cloud of moving dots moving along an ellipses with a motion that either violated or complied with the two-thirds power law. Stimuli complying with this motor invariant differentially activated a widespread network of areas that included several regions involved in action observation (Dayan *et al.*, 2007). In contrast, in the present study, observation of bodily movements complying with the two-thirds power law, when contrasted with movements violating this motor invariant, produced a more focused activation pattern involving only regions in the frontal lobe, mostly lateralized to the left hemisphere. Figs. 4 and S4 suggest that this difference might be due to the manner in which stimuli violating the two-thirds are processed by the brain in the two cases. The two figures show brain areas in the two studies respectively that were equally activated by the presented visual stimuli independently of their kinematics. As is evident from Fig. 4, many brain areas involved in action observation were equally active during observation of a moving body, independently of the compliance of its movements with the two-thirds power law. On the contrary, in the case of abstract motion stimuli, only a small subset of this network was equally activated by “normal” and “perturbed” stimuli. Thus, the comparison between the “normal” and the “perturbed” conditions yielded, in the case of bodily movements, a much more focused activation pattern. A possible reason underlying the widespread activation pattern yielded by computer generated characters whose movements violate the two-thirds power law is the interaction between two factors: body shape and movements resembling those of a human. Indeed, in our experiments, static pictures of the human body were sufficient to activate brain areas largely overlapping with the action observation network above baseline (Fig. S5b). Moreover, Fig. S5a shows that these activations are stronger, with respect to pictures of static bodies, when the displays contain bodily movements, even they do not comply with normal kinematic laws of human movements. In summary, taken together with our previous results, the present study reveals that the observation of a moving body, independently of its kinematics, is sufficient to activate many of the brain areas involved in action observation. This appears not to be the case for simple motion displays where stimuli violating the kinematics laws of human movements activated this network of areas in a weaker and much less widespread manner. The present findings and those reported in our earlier study suggest that, in addition to the preference for movements at a constant equi-affine speed or with smooth velocity profiles (see (Dayan *et al.*, 2007)), activation patterns obtained in the case of both simple motion displays complying with the two-thirds power law might be also due to top-down effects, e.g. the subjects' “*expectations*”.

The fact that specific brain structures are selectively activated by the two-thirds power law suggest that the recognition and discrimination of normal human kinematics have high ecological relevance. For example, under conditions of of low visual acuity, e.g. under low illumination or at the periphery of the visual field, when shapes are poorly recognizable a fast analysis of the kinematics of the perceived movement might be instrumental in discriminating biological motion against the background of non-biological motion, such as the shaking of a tree. Under natural conditions, this mechanism could be potentially important for survival.

In conclusion, our study demonstrates that regions in the left dorso-frontal and pre-motor cortex that are critical for action recognition, possibly by matching the observed movements with one's own motor programs, are differentially activated by human movements dependent on their compliance with kinematic invariants of human movements. The matching process seems thus to be critically dependent not only on the consistency between the body structure of the observer and actor, but also on the consistency with human kinematic laws of motion. Interestingly, in agreement with this proposal, psychophysical data show that differences in spontaneous interference effects between observed human and robotic actions on concurrently executed movements (Kilner, Paulignan & Blakemore, 2003) disappeared when the kinematic law of motion of the robotic movements was matched to the human one (Oztop, Franklin, Chaminade & Cheng, 2005). This result, per se, does not exclude that, in addition to motor expertise, also visual expertise might contribute to our sensitivity to human kinematics (Jastorff, Kourtzi & Giese, 2006). For example, recent psychophysical evidence shows that, under ecologically relevant conditions, visual familiarity plays a role in person identification from point-light displays (Jacobs, Pinto & Shiffrar, 2004), a task that relies on a fine analysis of kinematic cues. Indeed, given our extensive visual and motor exposure to the two-thirds power law it is possible that the recruitment of either type of expertise might depend on the particular task that the subjects have to carry out (Hiris, Krebeck, Edmonds & Stout, 2005). A third possibility, is that visual sensitivity to the two-thirds power law might reflect a specific tuning to fundamental geometric properties of the observed movements. Theoretical results show that the two-thirds power law is equivalent to moving at constant equi-affine speed (Pollick & Sapiro, 1997). Thus, the selective activations found in pre-motor areas during observation of bodily movements complying with the two-thirds power law might reflect a visual selectivity for movements that have a simpler description in an equi-affine rather than in an Euclidean coordinate system (Flash & Handzel, 2007; Pollick & Sapiro, 1997; Polyakov *et al.*, 2009). Additional experiments are needed in order to fully explore these three non-mutually excluding possibilities.

Acknowledgments This work was supported by the Deutsche Forschungsgemeinschaft [grant number SFB550-C10]; Human Frontier Science Program [grant number RGP0054/2004-C]; European Commission [COBOL Grant 043403]; the Volkswagenstiftung; and the Hermann and Lilly Schilling Foundation. Correspondence should be addressed to Antonino Casile (antonino.casile@uni-tuebingen.de)

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		MNI Coordinates			
Brain Areas	**Brodmann Area**	X	Y	Z	Z score
Normal > Perturbed					
L Middle Frontal Gyrus	6.8	-42	24	45	4.23
L Superior Frontal Gyrus	9	-21	45	39	4.17
L Middle Frontal Gyrus	8.9	-24	33	39	3.93
R Medial Frontal Gyrus	10	6	60	3	3.68
L Media Frontal Gyrus	10	-3	57	3	3.66
L Anterior Cingulate Gyrus	32	0	45	3	3.58
Perturbed > Normal					
	No activations were obtained				

Table 1 *– Foci of activity for the contrasts "normal > perturbed" and "perturbed > normal" respectively. Activations were thresholded at p<0.001 (uncorrected) at the single voxel level and at p<0.05 (corrected) at the cluster level.*

		MNI Coordinates			
Brain Areas	**Brodmann Area**	X	Y	Z	z-score
Button Press > NO Button Press					
L Insula	13	-39	9	15	5.1
L Medial Frontal Gyrus	6	-3	-12	51	4.44
L Pre- and Postcentral Gyrus	2.4	-54	-24	54	4.4
R Cerebellum Anterior Lobe		24	-54	-21	4.32
R Inferior Parietal Lobule	40	66	-36	24	4.28
L Cerebellum Anterior Lobe		-27	-48	-21	4.22
R Precentral Gyrus	44	48	3	9	4.1

Table 2 *– Foci of activity when contrasting BOLD responses in trials containing a button press with trials containing no button press. Activations were thresholded at p<0.001 (uncorrected) at the single voxel level and at p<0.05 (corrected) at the cluster level.*

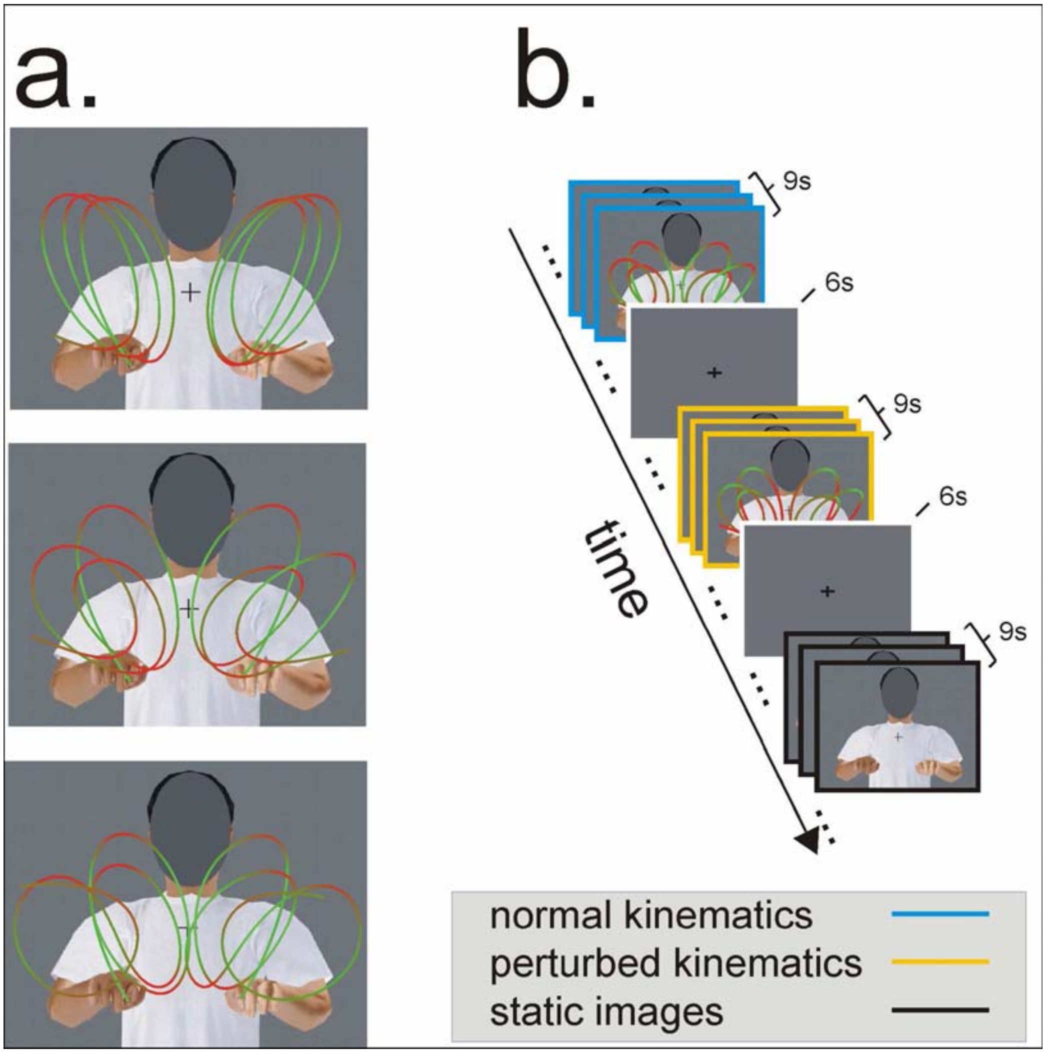

Figure 1 – *Biological motion stimuli and experimental paradigm. (a) Stimuli consisted of computer-generated animations depicting a person executing three types of curvilinear movements (roughly resembling the trigrams 'lll', 'lee' and 'leo') with both hands in the air. Hand trajectories were obtained by motion capturing of a human subject. In one set of stimuli ('**normal**'), the movements of the animated avatar were the original recorded movements and thus complied with the normal human kinematic laws of motion. A second set of stimuli ('**perturbed**') was created from the first one by means of non-linear time warping in order to destroy compliance with the two-thirds power law. The different colors along the trajectories represent the instantaneous hand velocity, with hues of red indicating points of lower velocity and hues of green indicating points of higher velocity. A third set of stimuli consisted of static snapshots of the animations ('**static**'). In all stimuli the face was occluded to minimize face-related neuronal activity. Each stimulus lasted for 3s. (b) Example of an experimental session. Each scanning session consisted of a sequence of trials of 9s during which three visual stimuli were shown consecutively followed by a 6s fixation interval. During each 9s trial only stimuli of one type ('normal', 'perturbed' or 'static') were shown. Trials were presented in a counterbalanced manner.*

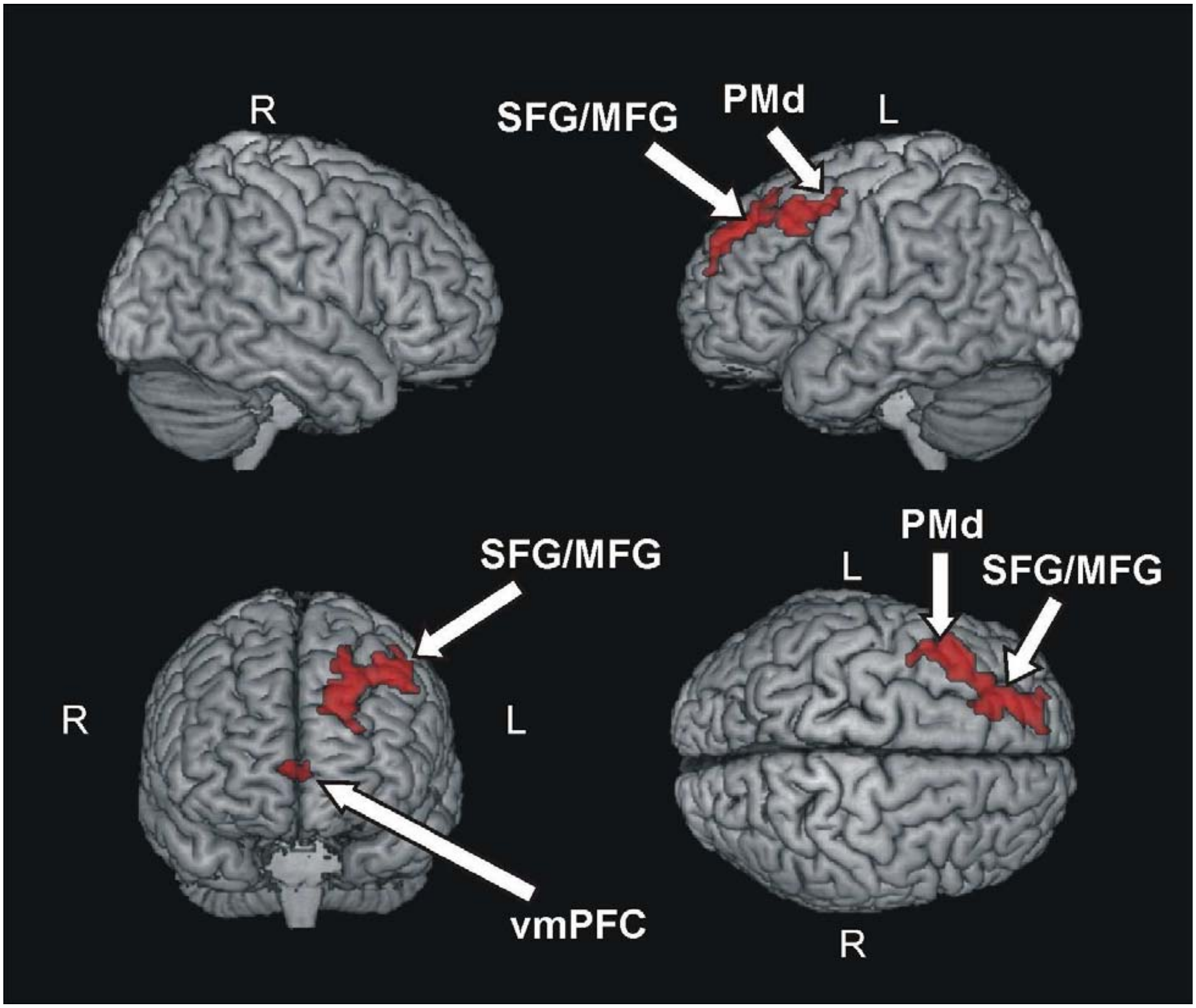

***Figure 2** – Brain areas showing higher BOLD responses during observation of human movements complying with normal kinematic laws of motion (see Table 1). Activations were thresholded at $p<0.001$ (uncorrected) at the single voxel level and at $p<0.05$ (corrected) at the cluster level. Abbreviations indicate: Superior Frontal Gyrus (SFG), Middle Frontal Gyrus (MFG), Pre-Motor dorsal (PMd) and ventro-medial Pre-Frontal Cortex (vmPFC).*

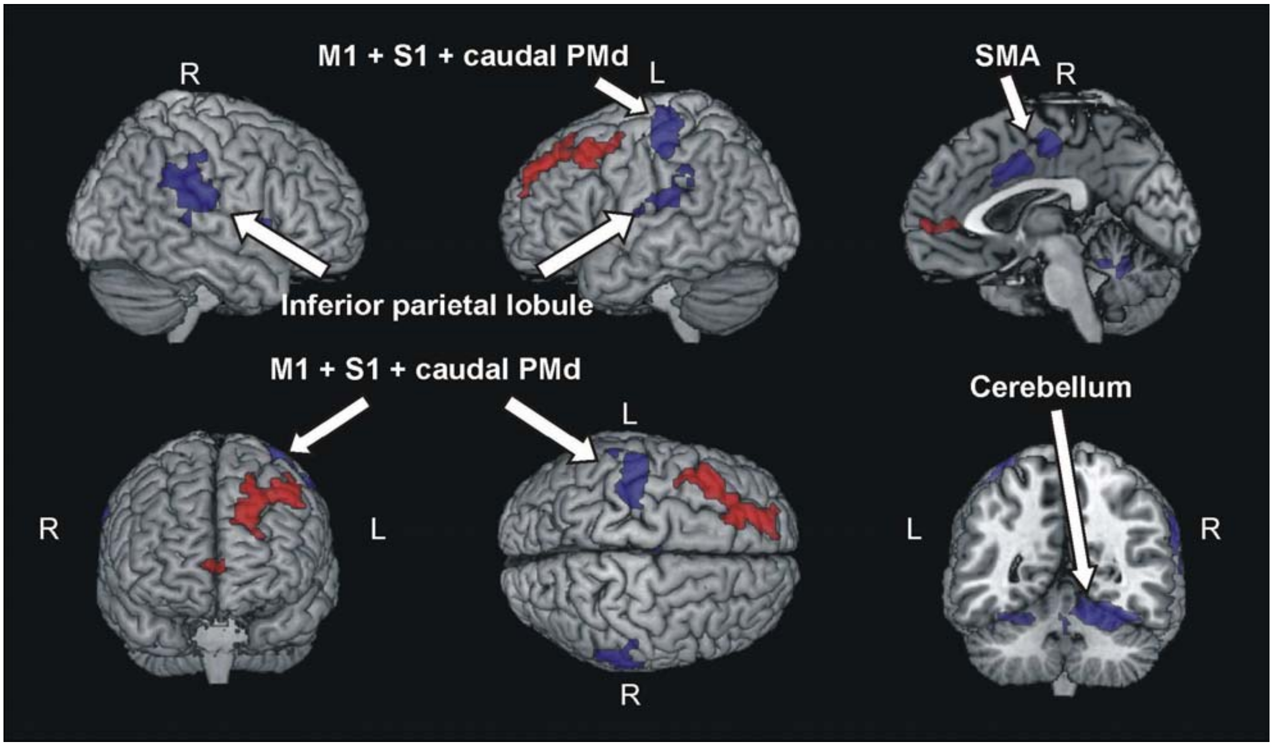

Figure 3 *– Brain areas showing higher BOLD response during trials containing button presses vs trials containing no button press (blue regions). Activations were thresholded at p<0.001 (uncorrected) at the single voxel level and at p<0.05 (corrected) at the cluster level. Abbreviations indicate: Primary Motor Cortex (M1), dorsal Pre-Motor Cortex (PMd), Primary Sensory Cortex (S1) and Supplementary Motor Areas (SMA). Brain areas that in the main experiment exhibited higher level of BOLD response for human movements complying with the two-thirds power law are plotted in red for comparison purposes (see also Fig. 2).*

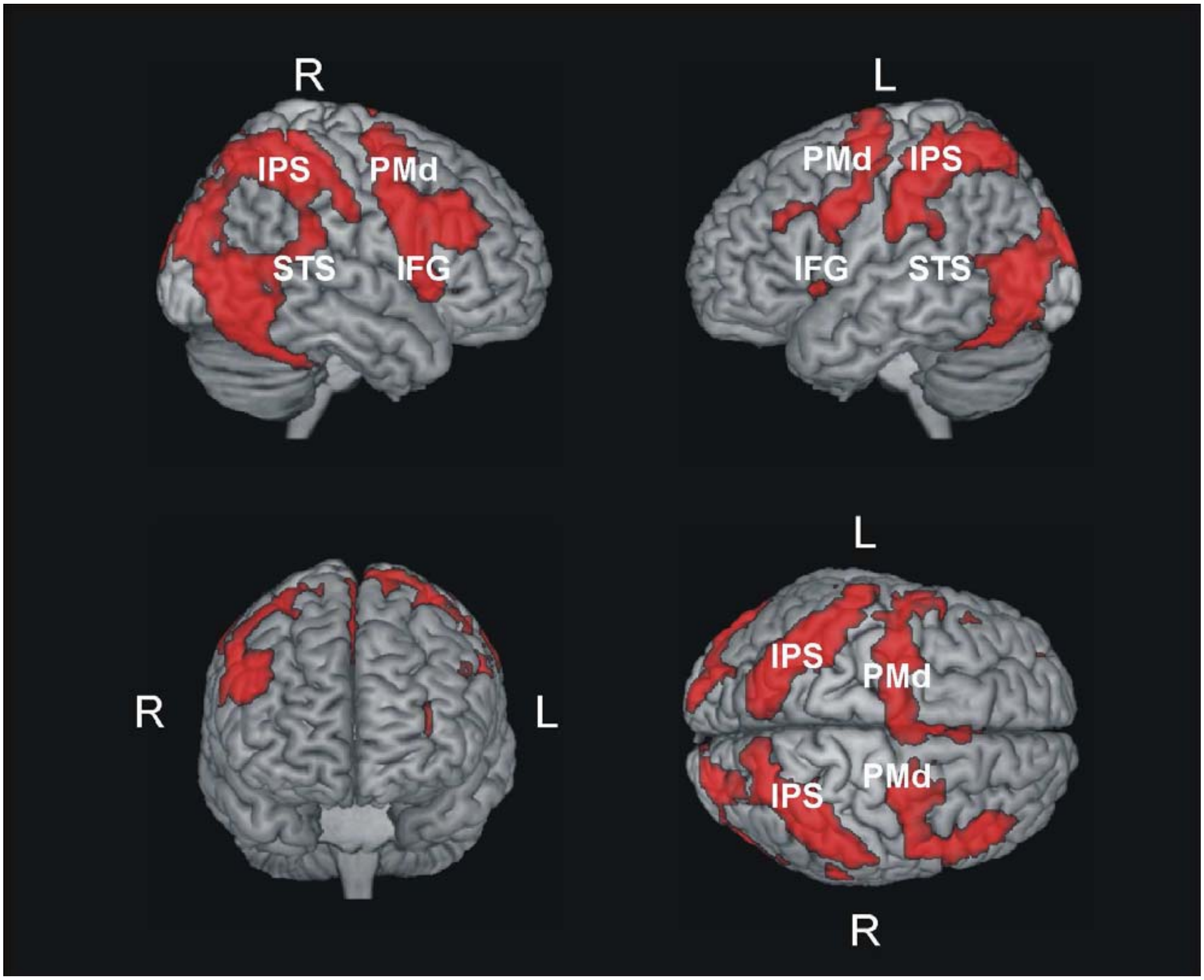

Figure 4 *– Brain areas activated by human movements independent of their compliance with normal kinematic laws of motion. The activation patterns in the figure were obtained by masking the contrast perturbed > baseline with the contrast normal > baseline. Prior to masking activations in both contrasts were thresholded at p<0.001 (uncorrected) at the voxel level and at p<0.05 (corrected) at the cluster level. Abbreviations indicate: PMd = Pre-Motor dorsal, IPS = Intra-Parietal Sulcus, STS = Superior Temporal Sulcus, IFG = Inferior Frontal Gyrus).*

Supplementary Material

Neuronal encoding of human kinematic invariants during action observation

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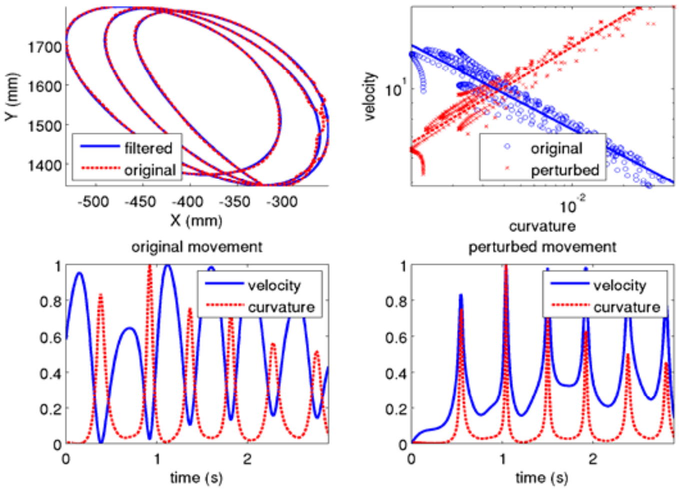
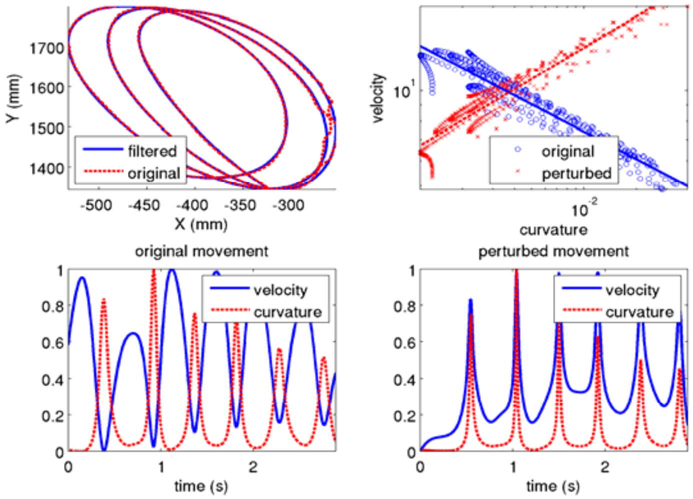


(a) Left Hand



(b) Right Hand

Figure S1 – *Perturbing the kinematics of human movements. The different panels show the kinematic characteristics of the original and "perturbed" hand trajectories for one of the movement (Trajectory 1 in Tables S1 and S2) used in our experiment. Data for the trajectories of the left and right hand are plotted in panels (a) and (b) respectively. In each panel the four figure signify the following: (upper left figure) raw (broken red line) and low-pass filtered (solid blue line) hand trajectories; (upper right figure) log-log plot of the instantaneous tangential velocity vs. curvature before and after applying the algorithm described in the Materials and Methods section for perturbing the slope of the two-thirds power law. The broken line indicate the best linear fit of the data; (lower figures) hand velocity (solid blue line) and curvature (broken blue line) of the path trajectory plotted as a function of time before (left figure) and after (right figure) perturbation of the slope of the two-thirds power law.*

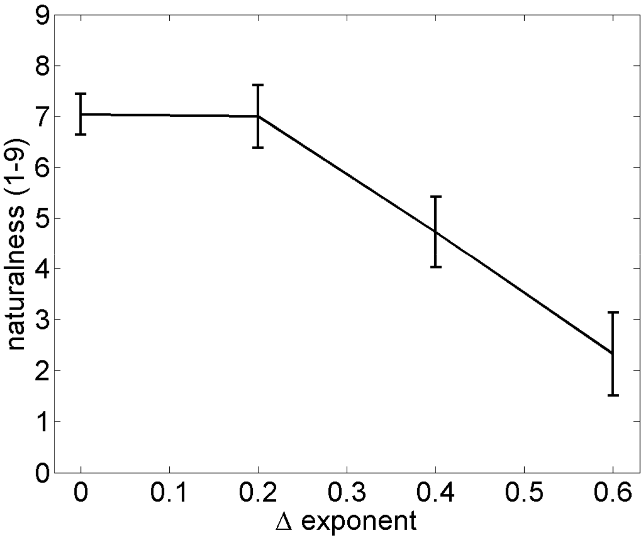


Figure S2 – *Results of a psychophysical experiment in which 6 subjects rated, in a scale from 1 (very unnatural) to 9 (perfectly natural), the naturalness of movements containing different degrees of perturbation of the two thirds power law. In the figure, the average rating is plotted as a function of the degree of perturbation of the exponent of the power law. That is, a value of 0 on the x axis indicates "normal" stimuli in our brain imaging experiment, whereas a value of 0.6 indicates the "perturbed" stimuli. Vertical bars represent standard errors.*

In each trial of the experiment, subjects were presented a movie showing a human-like avatar whose hand movements exhibited different degrees of compliance with the two-thirds power law. The task of the subjects was to rate in a scale from 1 to 9 the perceived naturalness of the movement. The hand trajectories and the method used to perturb the two-thirds power law were the same as those in the brain imaging experiment (see Materials and Methods in the main text). In this psychophysical experiment we presented visual stimuli having four different equispaced degrees of perturbation of the two-thirds power law ranging from a value of $\Delta=0$ (i.e. no perturbation) to a value of $\Delta=0.6$.

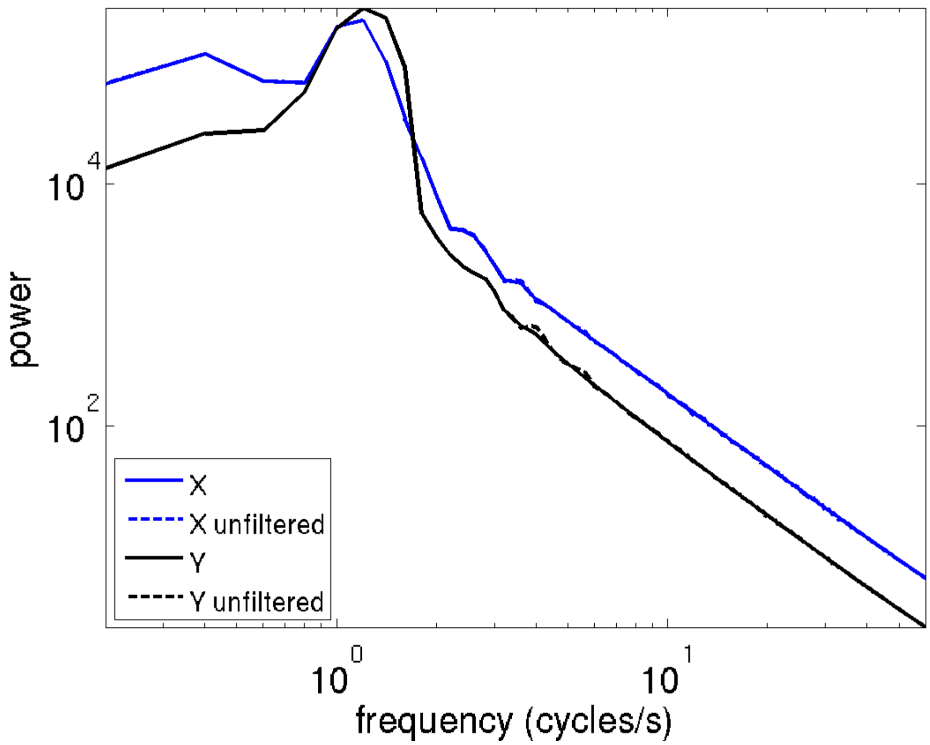


Figure S3 – *Frequency content of the motion captured hand trajectories used to animate the avatars. The curves represent the average power spectra of the hand trajectories along the horizontal (X) and vertical (Y) axes respectively. Solid lines represent power spectra of the low-pass filtered trajectories, whereas dashed line represent the power spectra of the original unfiltered trajectories.*

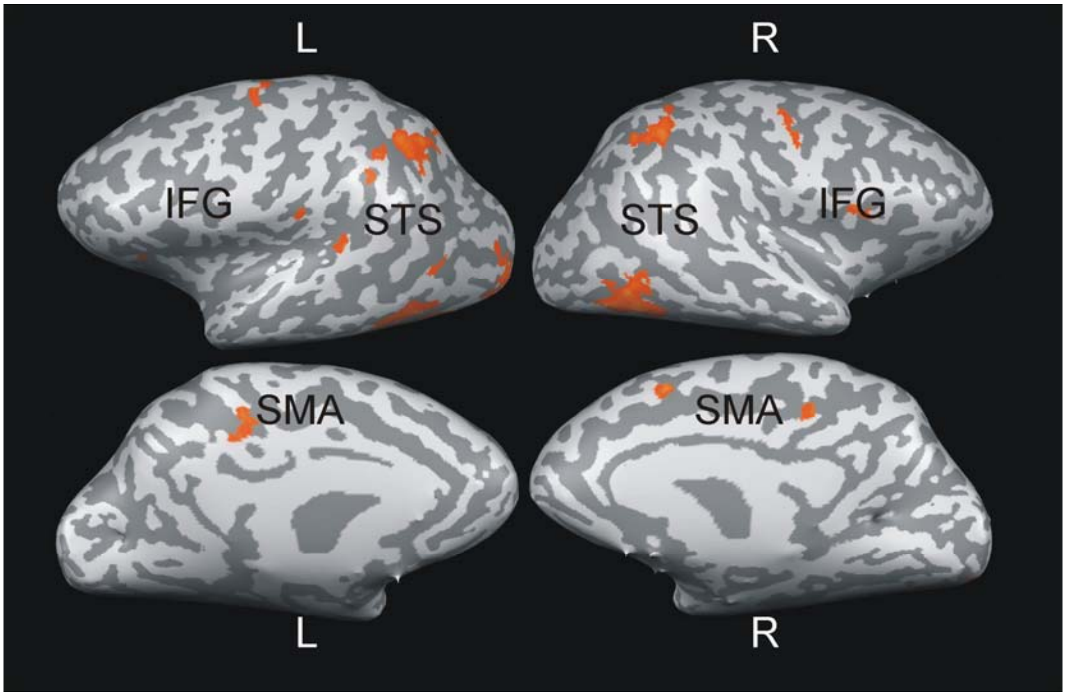


Figure S4 – *Brain areas activated by abstract motion displays independent of their compliance with normal kinematic laws of motion. The panels show the BOLD responses of a group of subjects during observation of a motion stimulus consisting of a cloud of dot moving along elliptical trajectories complying with ("normal") or violating ("perturbed") the two-thirds power law* (Dayan *et al.*, 2007)*. The activation patterns in the figure were obtained, similar to Fig. 4 in the main text, by masking the contrast perturbed-baseline with the contrast normal-baseline.*

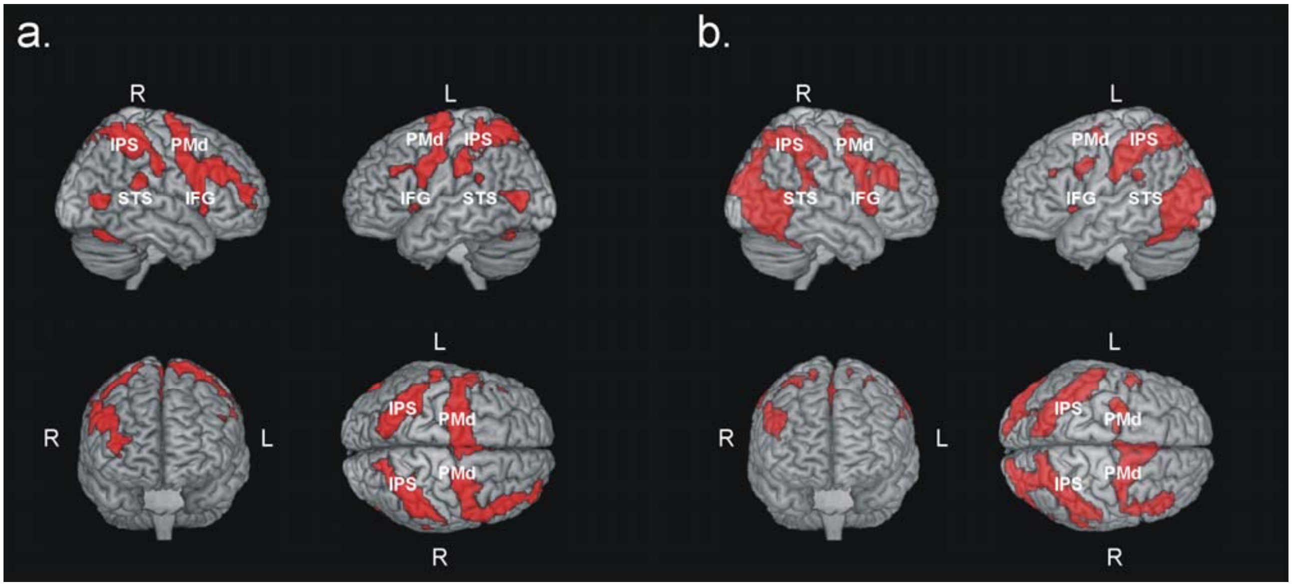


Figure S5 – *Brain areas activated by human movements independent of their compliance with normal kinematic laws of motion (panel a) and by static pictures of the human body (panel b) . The activation patterns in panel (a) were obtained by intersecting the two contrasts perturbed > static with the contrast normal > static whereas the activation patterns in panel (b) indicate brain areas that were significantly more active during observation of static pictures of the human body with respect to baseline activity. In both cases statistical maps were thresholded at p<0.001 (uncorrected) at the voxel level and at p<0.05 (corrected) at the cluster level. Abbreviations indicate: PMd = Pre-Motor dorsal, IPS = Intra-Parietal Sulcus, STS = Superior Temporal Sulcus, IFG = Inferior Frontal Gyrus).*

	Slope (tangential velocity vs curvature)				Duration
	Normal		Perturbed		
	Left Hand	Right Hand	Left Hand	Right Hand	
Trajectory 1	-0.29	-0.31	0.33	0.3	2.89s
Trajectory 2	-0.27	-0.3	0.35	0.31	2.5s
Trajectory 3	-0.3	-0.32	0.32	0.27	2.46s
Trajectory 4	-0.27	-0.29	0.37	0.33	2.79s
Trajectory 5	-0.29	-0.3	0.32	0.32	2.79s
Trajectory 6	-0.31	-0.33	0.28	0.28	2.21s
	-0.3±0.02		0.32±0.03		2.61s±0.26 s

Table S1 – *Characteristics of the hand movements used to generate the normal and perturbed stimuli used in the brain imaging experiment. The first two columns (“Normal”) show the estimated slope of the power law relating tangential velocity and curvature of the original motion captured hand trajectories. A value of -1/3 indicates compliance with the two-thirds power law. The third and fourth columns (“Perturbed”) show the estimated slope of the power law relating tangential velocity and curvature after the timing was modified as described in the main text. The rightmost column (“Duration”) shows the duration in seconds of each movement.*

	Tangential Velocity (min, average, max) in m/s			
	Normal		Perturbed	
	Left Hand	Right Hand	Left Hand	Right Hand
Trajectory 1	0.59, 1.15, 1.61	0.58, 1.08, 1.59	0.64, 1.15, 2.21	0.66, 1.08, 2.04
Trajectory 2	0.61, 1.09, 1.6	0.67, 1.04, 1.66	0.61, 1.09, 2.15	0.64, 1.04, 1.83
Trajectory 3	0.52, 1.08, 1.77	0.56, 0.96, 1.81	0.58, 1.08, 2	0.63, 0.96, 1.69
Trajectory 4	0.47, 1.11, 1.58	0.55, 1.05, 1.58	0.57, 1.11, 2.04	0.51, 1.05, 1.83
Trajectory 5	0.36, 1.07, 1.69	0.45, 1, 1.6	0.58, 1.07, 2.14	0.47, 1, 1.93
Trajectory 6	0.37, 1.24, 1.92	0.46, 1.18, 1.85	0.77, 1.24, 2.83	0.7, 1.18, 2.53
	0.49, 1.12, 1.69	0.55, 1.05, 1.68	0.62, 1.12, 2.23	0.6, 1.05, 1.97

Table S2 – *Kinematic characteristics of the hand movements used to generate the normal and perturbed stimuli used in the brain imaging experiment. The characteristics of different movements are shown on different rows. The bottom row shows the average values across movements. Each slot in the table shows the minimum, average (in red) and maximum value of the tangential velocity. Values used to animate stimuli used in the “normal” condition are shown in the first two columns, whereas data used to animate stimuli used in the “perturbed” condition are shown in the two rightmost columns.*

References

Dayan E, Casile A, Levit-Binnun N, Giese MA, Hendler T, Flash T. 2007. Neural representations of kinematic laws of motion: evidence for action-perception coupling. Proc Natl Acad Sci U S A. 104:20582-20587.