

Seeing or Doing? Influence of Visual and Motor Familiarity in Action Observation

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Summary

The human brain contains specialized circuits for observing and understanding actions [1–3]. Previous studies have not distinguished whether this “mirror system” uses specialized motor representations or general processes of visual inference and knowledge to understand observed actions [4]. We report the first neuroimaging study to distinguish between these alternatives. Purely motoric influences on perception have been shown behaviorally [5], but their neural bases are unknown. We used fMRI to reveal the neural bases of motor influences on action observation. We controlled for visual and knowledge effects by studying expert dancers. Some ballet moves are performed by only one gender. However, male and female dancers train together and have equal visual familiarity with all moves. Male and female dancers viewed videos of gender-specific male and female ballet moves. We found greater premotor, parietal, and cerebellar activity when dancers viewed moves from their own motor repertoire, compared to opposite-gender moves that they frequently saw but did not perform. Our results show that mirror circuits have a purely motor response over and above visual representations of action. We understand actions not only by visual recognition, but also motorically. In addition, we confirm

that the cerebellum is part of the action observation network.

Results and Discussion

Observing someone else’s action allows us to understand what the observed agent is doing. Two possible brain mechanisms have been proposed to explain this ability. On the one hand, the observer’s brain might contain a specialized system for understanding actions, based on representing the motor commands required to make the action. On the other hand, the brain might understand actions using the same general perceptual, inferential, and theory-building processes that are used to understand other objects and their interactions. Studies of “mind-reading,” in which subjects explicitly attribute beliefs to other people, make an analogous distinction between “simulation theory” and “theory theory” [6, 7]. However, these two alternative theories have rarely previously been distinguished for the fundamental case of understanding another person’s action [8]. It remains unclear whether the brain understands observed actions using a specialized system for motor representation, or using general principles of inference based on visual experience.

The human brain contains specialized parietal-premotor circuits (“mirror system”) that are activated when observing and understanding the actions of others [1–3]. However, previous studies have not distinguished whether these areas contain a truly motor representation, or simply general knowledge about the observed action. We present a crucial experiment that distinguishes between these theories for the first time. We show that observing an action evokes a purely motor representation. This cannot be explained by general processes of visual inference and knowledge.

We used a mixed factorial block-fMRI design to dissociate motor responses during action observation from those related to visual or theoretical knowledge associated with the action. Brain activity during observation of intransitive actions was compared between two groups of individuals who differ in motor skill but have similar visual experience of the observed actions. In classical ballet, some moves are gender specific (performed primarily by males or females), while other moves are common to both genders. However, all dancers are visually familiar with both types of move, since male and female dancers train and perform together over extensive periods of time. Therefore, all dancers have visual knowledge of all moves, but they have additional motor representations only for those specific to their own gender. We compared activity when male and female dancers viewed gender-specific moves performed by their own gender, compared to other gender-specific moves performed by the other gender. This enabled us to dissociate brain responses related to motor representation from those related to visual knowledge about the observed actions, allowing for a characterization of the

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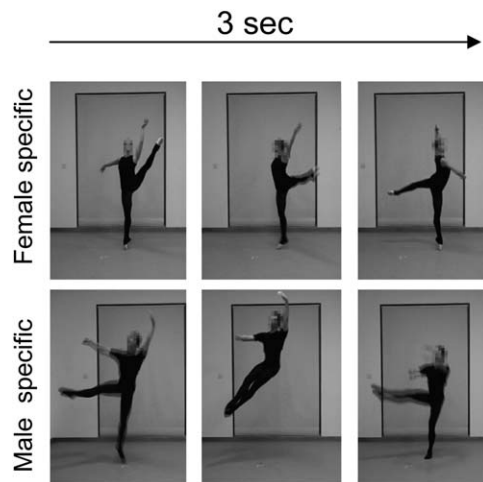


Figure 1. Dance Stimuli

Illustrative color 3 s videos of standard classical ballet moves that are female specific (top) and male specific (bottom). Eight different moves of each type were performed by professional female and male dancers and matched by a professional choreographer for kinematic features. The dancers' faces were blurred (for examples, see [Movies S1 and S2](#) in the [Supplemental Data](#)).

neural correlates of pure motor response during action observation.

Two groups of subjects, female and male professional ballet dancers, viewed the same set of movement stimuli. Subjects in each group viewed video clips of a male or female expert dancer performing *gender-specific* ballet moves (Figure 1; for examples, see [Movies S1 and S2](#) in the [Supplemental Data](#) available with this article online). In this 2 × 2 experimental design, the interaction between subject gender and the gender of the observed performer includes the effect of pure motor familiarity. However, it also includes a confounding effect of gender congruence: a subject watching a gender-specific move for which he or she has the motor skill must be watching someone of his or her own gender. To control for this confound, we also included additional *gender-common* stimuli, showing ballet moves routinely performed and

seen by both genders. The interaction between subject gender and performer gender for the gender-common moves gave an independent estimate of the confounding gender congruence effect. That is, for gender-specific stimuli, each subject had motor expertise for the moves performed by his or her own gender, but not for those performed by the other gender. There was no corresponding difference in motor expertise for the gender-common stimuli. The difference between the interaction terms for these two classes of stimuli provides a pure estimate of motor expertise effects.

Immediately after the scanning session, the subjects completed a subjective questionnaire in which they were asked how often they *do* and *see* the moves previously shown in the scanner. Subjects' ratings of their visual and motor familiarity (see [Figure 2](#) and [Supplemental Data](#)) confirm that subjects had equal *visual* experience with the gender-specific and the gender-common stimuli. In contrast, levels of motor experience depended clearly on the gender of the subject in the case of gender-specific actions, but not in the case of gender-common actions.

Functional images of brain activity during action observation were analyzed by statistical parametric mapping (SPM2) using a general linear model applied at each voxel across the whole brain. We fitted a factorial model including factors of subject gender (male/female), gender of the observed performer (male/female), and type of observed action stimuli (gender-specific/gender-common). The two-way interaction between subject gender and performer gender includes an effect of motor expertise in the case of gender-specific stimuli, plus a confounding effect of gender congruence. The same interaction for gender-common stimuli contains only the effect of gender congruence, since all subjects commonly make and see all the gender-common moves. Therefore, the difference between the two interaction terms, corresponding to the three-way interaction of subject gender, performer gender, and stimulus type, estimates the pure effect of motor expertise during action observation. Areas showing a significant three-way interaction included the left premotor cortex, the intraparietal cortex bilaterally, and the cerebellum bilaterally (Figure 3).

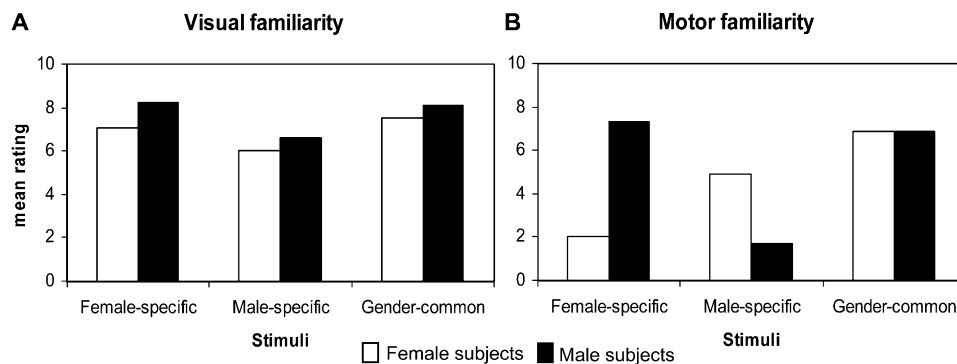


Figure 2. Ratings of Visual and Motor Familiarity

Subjects rated their visual and motor familiarity with each movie in a postscanning questionnaire (scale: 0 = completely unfamiliar, 10 = highly familiar) with the different classes of dance stimuli (female/male gender-specific moves and gender-common moves). For motor familiarity there was a significant interaction between gender of observer and type of move [$F(2,20) = 66.274$; $p < 0.001$]. The corresponding interaction was not significant for visual familiarity.

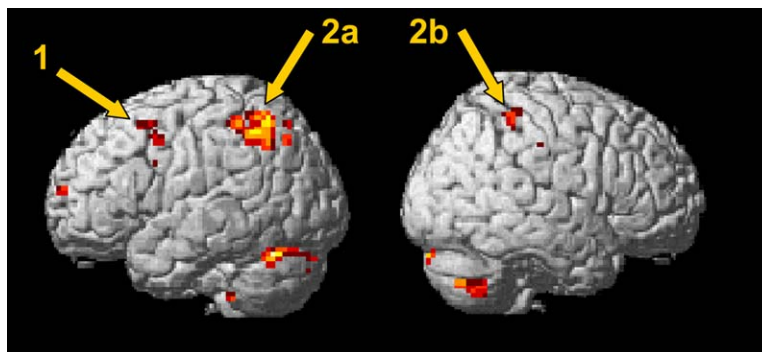


Figure 3. Effect of Motor Expertise on Action Observation

Activations shown are the interaction between subject gender and performer gender for gender-specific moves, minus the same interaction for common moves. This difference between two-way interactions reveals the additional activation associated when the subject observes a move for which he or she possesses the motor schemata, compared to observing moves for which he or she does not possess the motor schemata. Subtracting the interaction for gender-common moves controls for the possible confounding effect of observing someone of the same gender as oneself. Projections of the

activation foci on the surface of a standard brain (Montreal Neurological Institute [MNI]) at $p < 0.001$. Note that this projection renders onto the surface activity, which may in fact be located in the sulci. Arrows indicate activity in areas described as part of the mirror system: (1) left dorsal premotor cortex, (2a) left intraparietal sulcus, and (2b) right intraparietal sulcus.

To visualize *how* motor expertise influenced the activation of these areas, we separately calculated parameter estimates for the 2×2 interaction of subject and performer gender. This calculation was done for the gender-specific moves and for the gender-common moves. Subtracting the latter from the former gives a 2×2 set of parameter estimate *differences* related to motor expertise (Figure 4). These showed that experts had greater activation when observing the specific movements that they could perform than when observing movements that they were not used to performing. This produced a crossover interaction between subject gender and performer gender, even after subtracting any possible gender congruence effects, to obtain parameter estimate *differences* (Figure 4). Thus, while all groups saw the same stimuli, the mirror system areas of their brains responded to the stimuli in a way that depended on the observer's specific *motor* expertise. The parameter estimates show that motor expertise influenced brain activity of both male and female subjects in a similar way, though the influence was stronger for males than for females. These results show that observing an action can activate the corresponding motor representation. For example, the brain could perform an internal simulation of the specific motor program for the observed movement.

In addition, further activations (see Table S2) were found in the precuneus, the parahippocampal region bilaterally, and the left hippocampus. Similar activations were found and discussed in previous studies [9]: we therefore focus here on the activations in motor-related areas.

We show that the brain's response to seeing an action depends not only on previous *visual* knowledge and experience of *seeing* the action, but also on previous *motor* experience of *performing* the action. The observation of action involves matching to the individual's motor repertoire, and not only to a perceptual template. Our results strongly support the concept of motor simulation in the human mirror system. When we observe someone else's actions, several distinct mental representations may be involved. First, there may be purely *visual* representations of stimulus kinematics [10–12], of the agent's body [13, 14], and of any object that may be associated with the action [15]. A strong mirror hypothesis posits that viewing actions automatically evokes a further,

purely motoric representation of the *motor commands* for the observed action. Previous neuroimaging studies have not disentangled which of these representations is contained in the human mirror system. Human neuroimaging studies have used a wider range of observed actions, including simple actions such as grasping [16, 17], movement of different body parts [18], identical actions performed by different body parts [19], and meaningless symbolic actions [20, 21]. However, in each case, mirror system activation in these studies could be interpreted as a nonspecific visual response rather than a specifically *motoric* response.

The present study avoids these visual confounds. The dance movements studied here did not involve external objects. However, we found clear mirror system activation despite absence of object representation. This result agrees with previous studies showing parietal, premotor, and cerebellar activations during observation of meaningless, intransitive actions [20, 22].

We used expertise effects to separate the visual knowledge from motoric representations involved in action observation. When an individual learns a new skill, he or she acquires new perceptual and motor representations [23]. Expertise effects compare brain activity between individuals who have acquired such representations, and those who have not. Previous studies have aimed to use acquired motor skills [9, 24, 25] to investigate whether mirror areas contain a purely motoric representation of observed actions. These studies showed greater mirror activity when watching a movement whose motor representation had been acquired compared to watching those that had not. However, none of these studies dissociates the observer's motor skill level from his or her visual familiarity with the action stimulus observed. Thus, skill sensitivity in the mirror system could reflect either differences in the ability to simulate the observed action motorically or differences in visual familiarity with the stimulus. To qualify as a distinct functional neural system, mirror systems should perform motor simulation, and not mere visual recognition. Several neurophysiological studies, including recordings of single mirror neurons in the primate, are ambiguous on this point. One recent study reported a class of mirror neurons that develops a purely visual response to observed actions involving tools that the monkey itself does not use [4]. However, perceptual and motor

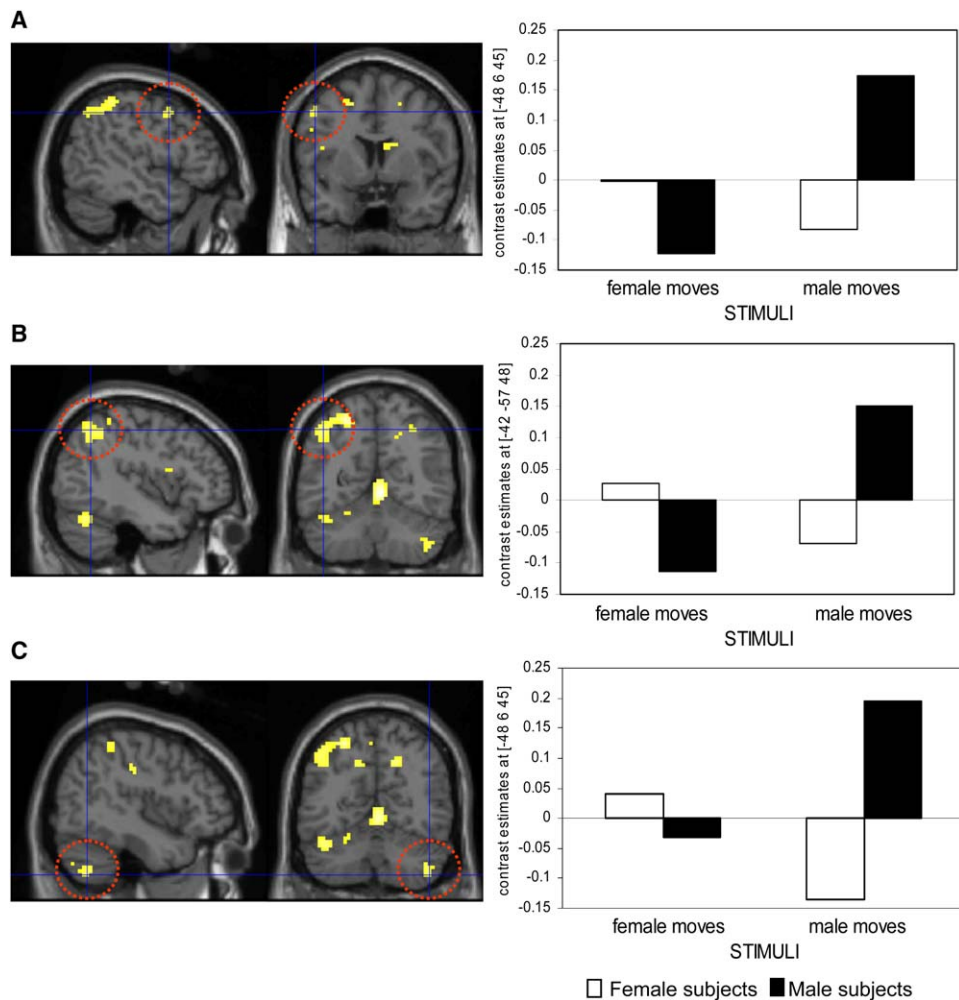


Figure 4. Sagittal and Coronal Sections and Parameter Estimates Showing Influence of Pure Motor Expertise in Action Observation

The effect of pure motor expertise was estimated using the difference between parameter estimates for the 2×2 interaction between subject gender and performer gender for gender-specific moves, and for the corresponding 2×2 interaction when viewing gender-common moves. Subtracting the interaction for gender-common moves controls for the confounding effect of observing someone of the same gender as oneself. Areas showing an effect of pure motor expertise ($p < 0.001$) include (A) left dorsal premotor cortex [-48 6 45], (B) left inferior parietal sulcus [-42 -57 48], and (C) right cerebellum [45 -60 -51]. Black bars show results for male observers, and white bars show results for female observers. The motor expertise effect is present for both male and female dancers but is stronger for males. This difference was not predicted and does not detract from the predicted relation between neural activity and motor expertise.

processes have been dissociated in a recent behavioral study [5]. There, learning a motor skill while blindfolded led to improved *visual* discrimination that was specific to the acquired motor pattern. Our design involved holding visual familiarity constant, while comparing individuals who differed in motor expertise. In our study, expertise refers to a very specific set of overlearned, stereotyped actions, rather than general differences in motor ability or motor differences between individuals or between species [26]. The motor representations evoked when our subjects viewed actions that they could perform could therefore be specific motor commands for each precisely characterized action sequence.

After controlling for the effect of visual familiarity with the observed actions, we found clear evidence for a purely motoric activation in three areas of the brain's motor network: premotor, parietal, and cerebellar cortices. The premotor and parietal activations agreed

closely with results of previous studies [18, 27, 28]. The premotor activation was strongest in the left hemisphere [16, 29], while the parietal activations were more bilateral [9]. Cerebellar activation has also been reported in fMRI studies of action observation [20, 26, 30–32]. However, it is rarely discussed, and to our knowledge, no primate studies have recorded from the cerebellum during action observation. Petrosini et al. [33] studied the ability of rats to learn new patterns of movement in a water maze by mere observation of another animal swimming in the maze. They found that cerebellar lesions impair this ability. We found bilateral cerebellum activations that resulted from motor simulation, suggesting a more extended action observation network than previously suggested by classical primate studies [2, 3].

We found no effects of motor expertise in temporal lobe areas concerned with visual expertise [34],

supporting the idea that our experimental design adequately controls for visual experience. We also found no effects in areas concerned with categorization and naming [35], suggesting that all subjects had equivalent semantic knowledge of all actions, despite differences in motor repertoire. Finally, we found no effects in the superior temporal sulcus (STS). This area was activated in biological motion [10–12] and some action observation studies [9, 24, 36]. The present study suggests that, when visual and motoric representations are clearly distinguished, the human STS represents visual rather than motoric aspects of actions.

Although the subjects in our experiment viewed actions of an individual dancing alone, their professional work requires an exquisite ability to observe the actions of others. This observation has a clear motoric aim, for example, in perfecting the dancer's own repertoire by watching a teacher, or in synchronizing with others in *pas de deux* or *corps de ballet* pieces. Motor simulation would clearly facilitate these aspects of dance skill.

To summarize, the present study clearly separates visual from motor components of action observation in the human brain for the first time. The visual aspect of viewing the human body is held constant, since all subjects saw the same stimuli. Although body perception processes may also depend on the bodily similarity between observer and observed, we controlled for any such effects by subtracting parameter estimates for gender-common actions from those for gender-specific actions danced by the same performers. Our results therefore show that mirror system activity depends on possessing the motor representation for an observed action, and not only on the visual knowledge of what is observed. This finding strongly supports the hypothesis that the motor-related areas of the brain simulate the commands for observed actions. These areas include the parietal, premotor, and cerebellar cortices. Individual differences in motor expertise provide a valuable means of separating visual aspects of action observation from truly motor representations.

Experimental Procedures

Subjects

Twenty-four professional ballet dancers from the London Royal Ballet (12 females, 12 males) participated in the study. All subjects were right handed with normal vision, had no past neurological or psychiatric history, and were aged 18–32. All gave written informed consent and were paid for their participation. The protocol was approved by the Ethics Committee of the Institute of Neurology, London.

Stimuli and fMRI Task

Color videos of standard classical ballet were recorded using a digital camera. The movements were performed by a male and by a female professional ballet dancer. The dancers were naive as to the purpose of the study. They wore similar garments and performed in front of the same background. Gender-specific female, male, and gender-common ballet moves were matched with the help of a professional choreographer according to criteria of speed, part of the body employed, body location in space, and direction of body movement. The choreographer selected those moves that achieved the best possible kinematic match between the different movement classes. Eight 3 s clips of each class of movement were selected and digitally edited. The dancers' faces were blurred to ensure that subjects processed body kinematics, rather than individual or emotional features (see Figure 1 and the Supplemental

Data for examples). The videos were presented on a screen situated outside the scanner, which the subject viewed via a mirror (20 × 12 cm) located inside the scanner. During the experiment, each video was repeated four times. Still images were used as a baseline condition.

Stimuli were presented in a block design. Subjects were instructed to indicate "how symmetric" they thought each video was by pressing one of three keys with three fingers of the right hand. This subjective judgment could be performed equally well on moving and static stimuli, and for all degrees of familiarity. To avoid motor preparation, assignment of buttons to response categories was randomized across trials. Previous training with this response schedule was performed outside the scanner with a second set of dance movies. Once the scanner session was finished, subjects completed a questionnaire to indicate their visual familiarity (question: "How often do you see this move?") or motor familiarity (question: "How often do you do this move?"). The questionnaire referred to each move shown in the experiment by its well-established name in classical ballet terminology. Subjects responded using a Likert scale between 0 (never) and 10 (very often). Questionnaire data were not available for one male dancer.

Scanning and Data Analysis

The fMRI data were acquired on a 1.5T Magnetom VISION system (Siemens). Functional images were obtained with a gradient echo-planar sequence using blood oxygenation level-dependent (BOLD) contrast, each comprising a full brain volume of 36 contiguous axial slices (2.5 mm thickness). Volumes were acquired continuously with a repetition time (TR) of 3.15 s. A total of 480 scans were acquired for each participant in a single session (20 min), with the first five volumes subsequently discarded to allow for T1 equilibration effects. During fMRI scanning, eye position was monitored online by an infrared eye tracker.

The data were analyzed using a general linear model in SPM2 (Wellcome Department of Imaging Neuroscience; <http://www.fil.ion.ucl.ac.uk/spm/>) implemented in MATLAB 6.5 Release 13. Individual scans were realigned, slice time corrected, normalized, and spatially smoothed by a 6 mm FWHM Gaussian kernel using standard SPM methods. The voxel dimensions of each reconstructed scan were 3 × 3 × 3 mm. Population inference was made through a two-stage procedure. At the first level we specified in a subject-specific analysis where the BOLD response was modeled by a boxcar waveform of 22 s representing a single block, convolved with a canonical hemodynamic response function plus temporal and dispersion derivatives. Statistical parametric maps of the t statistic were generated for each subject, and the contrast images were stored.

In a second level random effects analysis, we used a 2 × 2 × 3 (subjects [male, female], actors [male, female], stimuli [gender moves, common moves, static image]) ANOVA model. We constructed a t contrast to test for a three-way interaction to find areas showing increased activity with motor familiarity. We defined *motor familiarity* as the interaction of interest (subject gender × gender of observed actor for gender-specific moves) minus the interaction (subject gender × gender of observed actor for gender common moves). This subtraction controls for the confounding effect of seeing someone of the same gender. Plots of parameter estimates were used to characterize whether the pattern of interaction reflects an effect of motor expertise. The surviving activated voxels were superimposed on high-resolution structural magnetic resonance (MR) scans of a standard brain (Montreal Neurological Institute, MNI). Anatomical identification was performed with reference to the atlas of Duvernoy [37].

Supplemental Data

The Supplemental Data include two tables and two examples of the videos used as stimuli in the experiment and can be found with this article online at <http://www.current-biology.com/cgi/content/full/16/19/DC1/>.

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