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Specificity of Action Representations in the Lateral Occipitotemporal Cortex

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Disciplines
Psychology

Specificity of Action Representations in the Lateral Occipitotemporal Cortex

Joseph W. Kable* **and Anjan Chatterjee**

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INTRODUCTION

A prominent theory of cortical organization divides higher level visual areas into a dorsal processing stream (involving occipitoparietal areas) that is important for visual control of motor behavior and a ventral processing stream (involving occipitotemporal areas) that is important for visual recognition and identification (Goodale & Milner, 1992). Most of the work establishing the ventral stream's role in visual recognition has focused on the recognition of objects. For example, functional imaging studies have identified areas within the ventral stream that respond preferentially to different categories of objects (Hasson, Harel, Levy, & Malach, 2003; Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997), and neuropsychological investigations have demonstrated that damage to ventral occipitotemporal areas impairs the ability to recognize objects (Ferreira, Ceccaldi, Giusiano, & Poncet, 1998; Schwartz, Barrett, Crucian, & Heilman, 1998; Goodale & Milner, 1992). However, humans can recognize classes of visual stimuli other than objects, such as actions, and deficits in action and object recognition can dissociate after brain damage (Ferreira et al., 1998; Schwartz et al., 1998; Rothi, Mack, & Heilman, 1986). In particular, damage to ventral occipitotemporal areas can impair object recognition while leaving action recognition intact. Given the critical role that action recognition plays in cognitive development and social cognition, it is important to understand the neural mechanisms of action recognition and how these might differ from those of object recognition.

One prominent hypothesis is that the understanding of actions is ''embodied.'' According to this view, the recognition of actions depends on mirror neurons within frontal and parietal cortices, which are active both when an individual engages in a certain action and when that individual sees the same action (Rizzolatti, Fogassi, & Gallese, 2001). However, this view cannot completely account for action recognition because individuals can recognize actions that they cannot perform themselves. For example, an inability to swim does not prevent one from being able to recognize someone else swimming. In addition, some action events, such as ''swarming bees,'' can be recognized although these actions cannot in principle be embodied in human motor systems. Finally, even for the view that action recognition is instantiated in mirror neurons, the question remains open as to whether the source of visual information for these circuits is sufficient in and of itself to recognize actions.

Several recent functional imaging studies have investigated the neural mechanisms of action recognition by comparing brain responses to action movies depicting moving human bodies to stationary pictures of human bodies or other objects (Rizzolatti et al., 2001; Allison,

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Puce, & McCarthy, 2000; Decety & Grezes, 1999). These studies generally find activation in a distributed network that includes lateral occipitotemporal, inferior parietal, and inferior prefrontal areas. The inferior parietal and prefrontal activations are consistent with the ''embodied'' hypothesis of action recognition. Furthermore, inferior prefrontal activity only occurs when the actions belong to the motor repertoire of the observer, whereas lateral occipitotemporal activity occurs whether or not the actions can be embodied by the observer (Buccino et al., 2004). This finding suggests that prefrontal and parietal cortices are involved in the recognition of actions through mirror neuron circuits, whereas the lateral occipitotemporal cortex is involved in the recognition of actions based on visual information alone. However, the exact role of the lateral occipitotemporal region remains unclear. Areas in the superior temporal sulcus are sensitive to biological motion (Grossman et al., 2000; Bonda, Petrides, Ostry, & Evans, 1996; Howard et al., 1996), and more posterior lateral occipital areas are sensitive to motion generally (Tootell et al., 1995) or to the human form (Downing, Jiang, Shuman, & Kanwisher, 2001). Thus, in comparing action movies and stationary images, greater activity in lateral occipitotemporal areas could be explained simply by the presence of different kinds of motion or of the human form, rather than the processing of actions per se. If these areas are truly involved in action recognition, then activity patterns in these regions should be action-specific—abstracting actions from the agents involved and distinguishing between different actions.

To investigate whether the lateral occipitotemporal cortex exhibits action-specific activity, we took advantage of the observation that repeated stimuli, compared to completely novel stimuli, are generally associated with decreased functional magnetic resonance imaging (fMRI) activity in areas processing these stimuli (Henson, 2003; Grill-Spector & Malach, 2001; Schacter & Buckner, 1998; Wiggs & Martin, 1998). These repetition-related decreases, often referred to as neural adaptation effects, are observed with stimuli repeated immediately or after delays ranging from minutes to days. Although the precise neuronal mechanisms underlying adaptation effects are still a matter of ongoing investigation (Henson, 2003; Grill-Spector & Malach, 2001; Wiggs & Martin, 1998), some investigators have recently shown that adaptation seen with immediate (Epstein, Graham, & Downing, 2003; Kourtzi & Kanwisher, 2001; Grill-Spector et al., 1999) and delayed (Dobbins, Schnyer, Verfaellie, & Schacter, 2004; James, Humphrey, Gati, Menon, & Goodale, 2002; Vuilleumier, Henson, Driver, & Dolan, 2002; Koutstaal et al., 2001) repetitions can be used to probe how different brain areas process specific aspects of stimuli. In addition to repeated and novel stimuli, these investigators also presented stimuli that were similar on one dimension while differing on another, compared to those seen previously. An adaptation effect for this condition then provided evidence that activity in an area was sensitive to the shared dimension and was not sensitive to the changed dimension.

In the present study, we used neural adaptation to dissociate responses specific to the action from responses to other components of action stimuli. During scanning, subjects watched short (2 sec) action movies while performing a speeded judgment about each movie that focused their attention on the actions depicted. In the critical scans, subjects saw four kinds of movies presented in a rapid, event-related fashion (see Figure 1): (1) the exact same movies they had seen in previous scans, (2) movies of people they had seen previously performing new actions, (3) movies of new people performing actions they had seen previously, and (4) movies in which both the people and the actions were new. We expected that many areas would show adaptation for repeated presentations of the exact same movies compared to completely novel movies (repetition adaptation: Old Person, Old Action < New Person, New Action). However, areas specifically involved in processing actions should also show adaptation for movies of previously seen actions performed by new people (action-specific adaptation: New Person, Old Action < New Person, New Action). Such action-specific adaptation implies that an area is sensitive to the *particular* action presented because only action identity differentiates the two conditions. Such an effect also demonstrates that activity in an area generalizes over different exemplars of the same action. Thus, action-specific adaptation would provide strong evidence that an area participates in action recognition and could not be explained by differences in the complexity of the stimuli, such as the presence of motion (biological or not) or the human form.

With these considerations in mind, we focused our analyses on the three functionally identified regions of interest (ROIs) on the lateral occipitotemporal surface (see Figure 2): a region in the superior temporal sulcus responsive to biological motion (pSTS) (Grossman et al., 2000; Bonda et al., 1996; Howard et al., 1996), the human homolog of motion-sensitive regions in the macaque (MT/MST) (Tootell et al., 1995), and a recently identified region near MT/MST that selectively responds to pictures of human bodies (extrastriate body area [EBA]) (Downing et al., 2001). Finding action-specific adaptation in any of these areas would establish that activity there distinguishes between particular actions and generalizes over different exemplars of the same action, a sensitivity that goes beyond the established responses in these three regions to the presence of different kinds of motion or of the human form. For a control comparison, we also tested two object-selective regions in the ventral occipitotemporal cortex, the fusiform face area (FFA) (Kanwisher et al., 1997) and parahippocampal place area (PPA) (Epstein & Kanwisher,

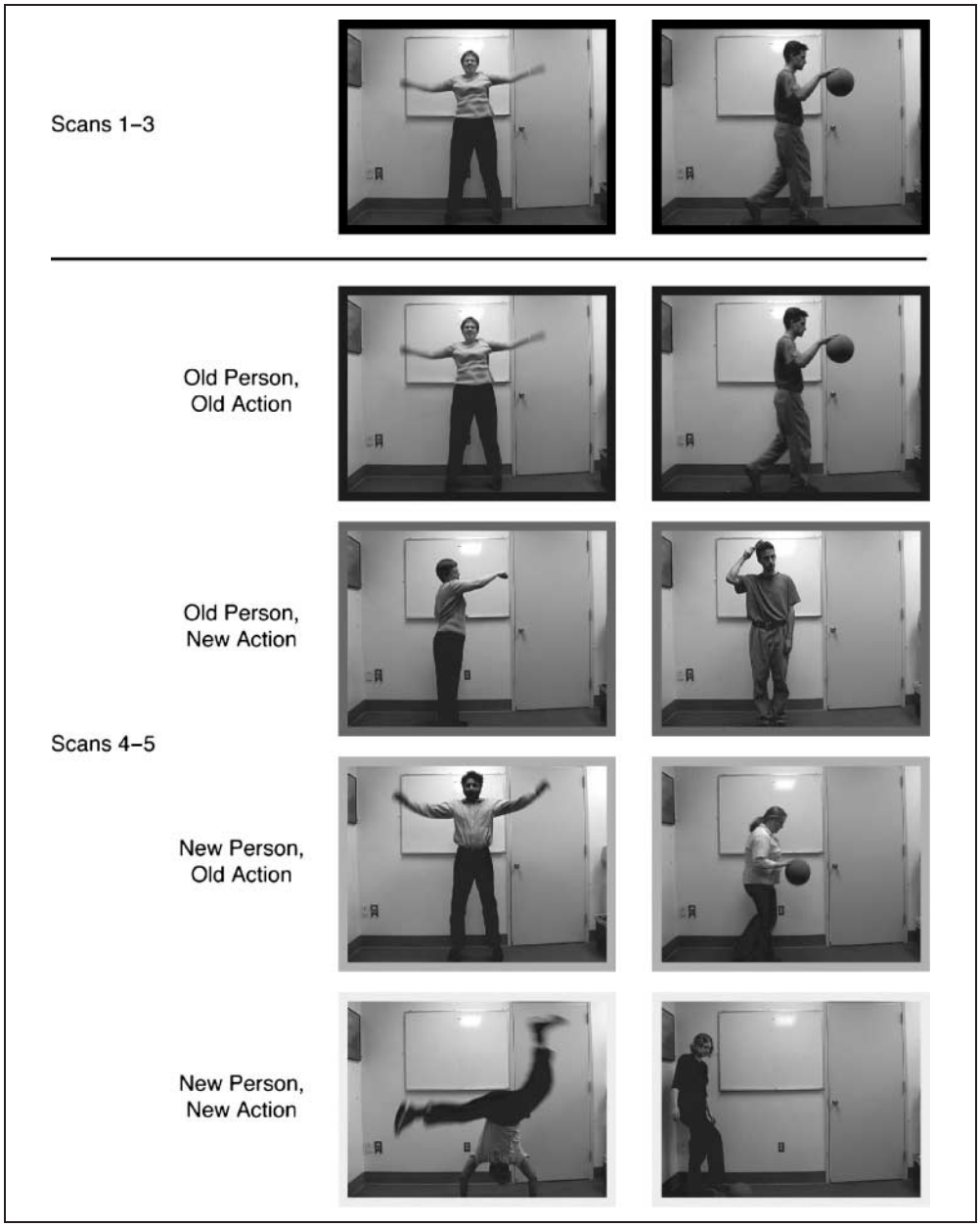


Figure 1. Action sequence stimuli and adaptation conditions. Single frames from action movie sequences used in the experiment are shown to illustrate the various adaptation conditions. (Top) During the first three scans, subjects saw the same set of movies repeated five times. (Bottom) During the last two scans, subjects saw (1) the exact same movies they had seen in previous scans (Old Person, Old Action), (2) movies of people they had seen previously performing new actions (Old Person, New Action), (3) movies of new people performing actions they had seen previously (New Person, Old Action), and (4) movies in which both the people and the actions were new (New Person, New Action).

1998), as well as an object-selective region that is part of the lateral occipital (LO) complex (Hasson et al., 2003). Finally, to detect any effects that might occur outside of these functionally defined regions, we also performed a whole-brain analysis.

METHODS

Subjects

Nine paid volunteers participated in the experiment (five women, four men; mean age = 23 years). All subjects were right-handed and spoke only English before school age. None had a history of neurological or psychiatric symptoms. All subjects gave informed consent in accordance with the procedures of the Institutional Review Board of the University of Pennsylvania.

Experimental Design and Stimuli

Each subject participated in at least eight functional scans. During the first five scans, subjects watched movies (2 sec in length, 30 frames/sec) in which a single person performed a recognizable action. In the first three scans, the subject was preexposed to a single set of 32 movies. During the first scan, these movies were presented in a sparse, event-related manner (one movie every 17 sec). This scan was used to estimate the in-

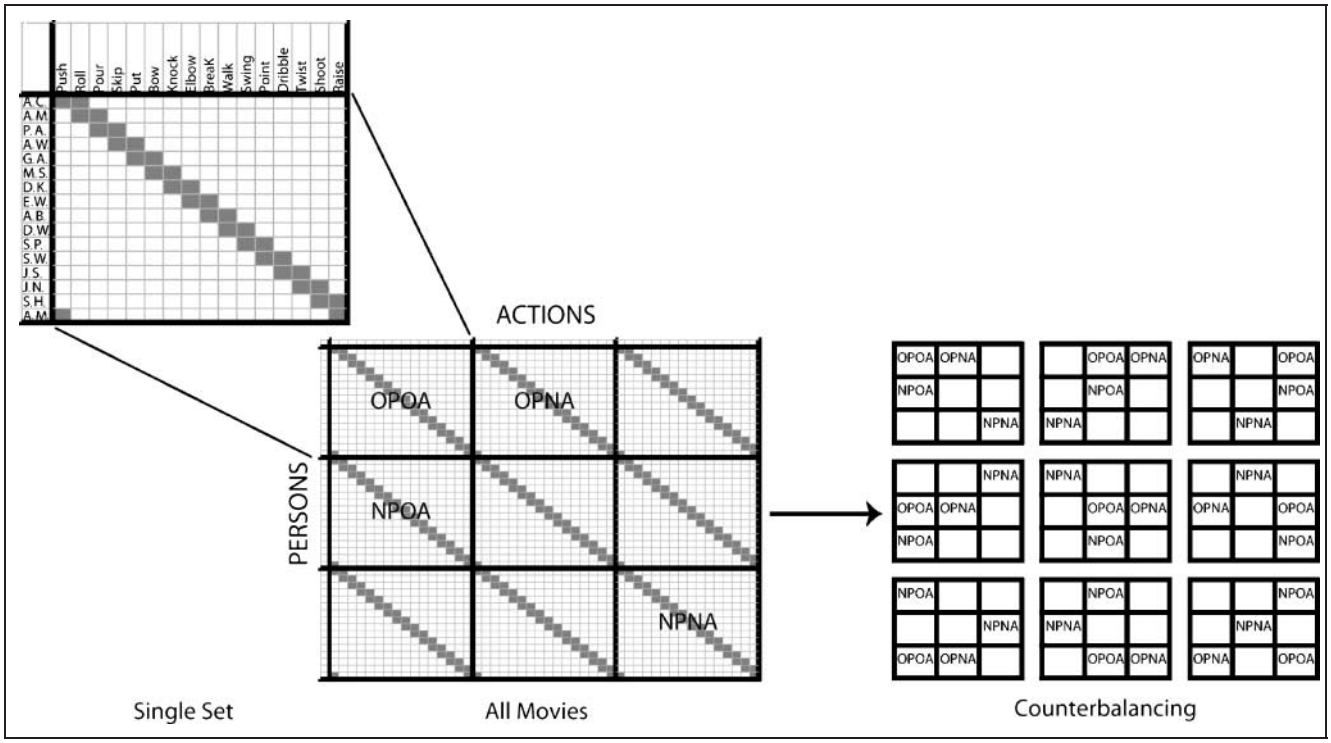


Figure 2. Stimulus sets and counterbalancing procedures. To ensure that any differences across adaptation conditions could not be attributed to idiosyncratic features of particular movies, the stimuli were precisely counterbalanced so that each movie appeared once in each of the four adaptation conditions across nine subjects. A single set of 32 movies is shown at the left. Each column represents a different action and each row represents a different person. Gray boxes indicate the action–person combinations used in this set. Within each set, each action or person appeared in two movies, so that a total of 16 different actions and 16 different people were represented in a single set. The complete stimulus set is shown in the center, which consisted of 288 different movies, composed of a combination of 48 actions and 48 people, divided into nine sets of 32 movies. The sets used in each of the four adaptation conditions for one subject are labeled in the center and shown schematically for all nine subjects at the right. OPOA = Old Person, Old Action; NPOA = New Person, Old Action; OPNA = Old Person, New Action; NPNA = New Person, New Action.

trinsic temporal autocorrelation for each subject, as well as a subject- and task-specific hemodynamic response function. During the second and third scans, the same set of movies was presented in a rapid event-related manner, with each movie being presented four times. Movies were presented every 4 sec, and presentations were jittered by interspersing 4-sec blank periods. Then, during the critical fourth and fifth scans, four sets of movies were presented in a rapid, event-related manner (see Figure 1): (1) the same set of movies used in the first three scans (''Old Person, Old Action''), (2) a set of movies with the same people seen in the first three scans performing new actions (''Old Person, New Action''), (3) a set of movies with new people performing the same actions seen in the first three scans (''New Person, Old Action''), and (4) a set of movies in which both the people and the actions were new (''New Person, New Action'').

Thus, each subject saw a total of 128 different movies from four different sets of 32 movies. The complete stimulus set and counterbalancing procedures are described in Figure 2, and a complete list of the actions used is provided in the Appendix. Each set of movies contained equal numbers of common (typically seen at least once a week) and uncommon actions, equal numbers of transitive (involved the use of an object) and intransitive actions, and equal numbers of male and female actors. Critically, across nine subjects, nine sets of movies were perfectly counterbalanced so that each set appeared once in each of the four different conditions. This counterbalancing ensured that any differences between the four conditions could not be attributed to idiosyncratic features of particular movies.

Subjects performed a speeded judgment for each movie, deciding whether the action in the movie was common (observed at least once a week) or not. Subjects were allowed a 2-sec time window to make their judgment. Because our primary motivation was to identify the neural mediation of action representations, we chose a task that (1) ensured that subjects attended to the action in the movie clip and (2) was applicable to a variety of different actions. Subjects' reaction times for this speeded judgment also provided a behavioral measure sensitive to their efficiency at action recognition, allowing us to investigate the relationship between behavioral priming and neural adaptation.

Because the common/uncommon judgment was inherently subjective (e.g., athletes might see someone kicking a ball at least once a week, whereas nonathletes might not), we did not classify subjects' responses as correct or incorrect. In lieu of accuracy, however, we calculated two measures based on subjects' responses that indicated how reliably they performed the task. First, we calculated how often subjects' responses agreed with the typical response for each action. The typical response for each action was determined by a rating study we performed before constructing the stimulus set, in which 15 subjects rated a larger list of actions as common or uncommon. For all of the actions used in the current experiment, at least two thirds of these subjects (10 of 15) agreed on a common/uncommon designation, with the mean agreement being 86 ± 2% (~13 of 15 subjects). Second, as described in Figure 2, the same action appears twice in each set of 32 movies. This allowed us to determine whether subjects made consistent responses by calculating how often subjects' made the same response for both exemplars of an action within a set.

After the first five scans, subjects also participated in localizer scans to functionally identify six ROIs (see Figure 3). To identify visual areas showing category-specific responses (FFA, PPA, LO, EBA), subjects participated in two scans during which they viewed 18-sec blocks of pictures from the following categories: natural landscapes (''places''), faces, objects, body parts (heads or faces not shown), and object pictures that had been scrambled. Each picture was presented for 400 msec with a 500-msec interstimulus interval. Subjects monitored the pictures for immediate repetitions, which occurred twice in each block.

Subjects participated in a single scan to identify the biological motion area in the superior temporal sulcus (pSTS) and the MT/MST complex. Subjects were shown 18-sec blocks of the following: ''point-light'' movies that were perceived as human movements (walking, jumping, kicking, etc.); movies of dots with the same motion vectors but with scrambled starting positions, so that no human form or movement was perceived; and stationary dots, taken from the first frame of the scrambled movies. Each movie was 1 sec in length (20 frames/sec), with a 2-sec interstimulus interval. Subjects were again monitored for immediate repetitions, which occurred once per block.

Data Acquisition

Data were acquired on a 3.0-T Siemens Trio scanner using a USA Instruments four-channel head coil. Blood oxygenation level dependent (BOLD)-sensitive, T2*-weighted functional images were acquired in 3-mm isotropic voxels using a gradient-echo, echoplanar pulse sequence (TR = 3000 msec, TE_{eff} = 30 msec). Forty 3-mm slices were acquired during each repetition, with

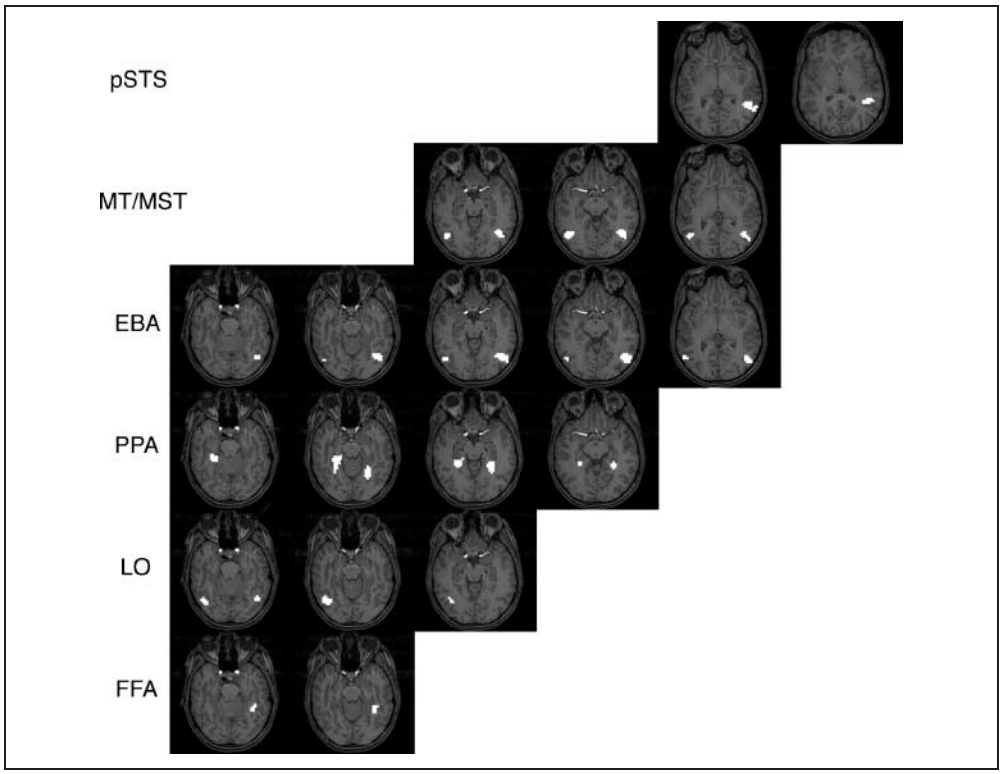


Figure 3. Functional ROIs. The locations of the six functionally identified ROIs are shown for one subject from the experiment. PPA = parahippocampal place area; FFA = fusiform face area, LO = lateral occipital object-selective area; EBA = extrastriate body area; MT/MST = human motion-sensitive cortex or V5, pSTS = superior temporal sulcus biological motion area.

each slice containing a 64 × 64 matrix within a 192 × 192-mm field of view. Head motion was minimized by using foam padding, and the scanner performed both prospective (3-D prospective acquisition correction [PACE]) and retrospective motion correction online. The number of images collected during each functional scan varied from 120 to 194, with the length of each scan thus varying from 6 min to 9 min 42 sec. The first six images of each functional scan were discarded to allow for steady-state magnetization to be achieved. High-resolution, T1-weighted anatomical images were also acquired for each subject by using an MPRAGE pulse sequence (TR = 1620 msec, TE = 3 msec, TI = 950 msec). One hundred sixty 1-mm slices were acquired, with each slice containing a 256 × 256 matrix within a 250 × 250-mm field of view.

A computer outside the scanner room controlled stimulus timing and response recording. Stimuli were projected onto a screen at the back of the scanner bore and viewed by subjects through a mirror mounted on the head coil. Subject responses were transmitted by a custom-designed fiber-optic response pad.

Data Analysis

Data analysis was performed with Voxbo software (www.voxbo.org). After image reconstruction, functional time series were sinc-interpolated in time to correct for staggered slice acquisition, realigned to the first image acquired for each subject by a six-parameter rigid-body transformation, and thresholded to exclude extraparenchymal voxels from subsequent analyses. Within each subject, a voxelwise analysis was performed with a modified version of the general linear model for serially correlated error terms (Aguirre, Zarahn, & D'Esposito, 1997; Zarahn, Aguirre, & D'Esposito, 1997; Worsley & Friston, 1995). Included in this model were covariates modeling different task conditions, a subject-specific estimate of the intrinsic temporal autocorrelation, and sine and cosine regressors for frequencies below those of the task (below 0.005 Hz for main analyses, below 0.0058–9.0179 Hz for localizer analyses) and for frequencies in the elevated range of the noise spectrum (above 0.1666 Hz). Task covariates were delta functions (main analyses) or boxcar waveforms (localizer analyses) convolved with a subject- and task-specific estimate of the hemodynamic response function (main scans) or a generic estimate empirically derived from the motor cortex in a large group of subjects (localizer scans) (Aguirre, Zarahn, & D'Esposito, 1998). Data from localizer scans were also smoothed in space with an 8-mm full-width half-maximum kernel and smoothed in time with the hemodynamic response function. The subject- and task-specific estimate of the hemodynamic response was derived from first scan of each subject (which involved the first presentation of Old Person, Old Action movies in a sparse, event-related manner) by averaging the response across all trials in all significantly modulated voxels.

From the localizer scans, we identified six ROIs in accordance with previous studies (Hasson et al., 2003; Downing et al., 2001; Grossman et al., 2000; Epstein & Kanwisher, 1998; Kanwisher et al., 1997; Tootell et al., 1995). ROIs were defined as contiguous voxels in a particular region showing greater activity for a specific contrast. FFA was defined based on the contrast of faces versus objects, PPA on the contrast of places versus faces and objects, LO on the contrast of objects versus faces and places, EBA on the contrast of body parts versus objects, pSTS on the contrast of point-light motion and random motion, and MT/MST on the contrast of random motion and stationary dots. Because this localizer for MT/MST differed slightly from one we had used previously (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002), we confirmed in seven of the current subjects that localizing MT/MST with moving and stationary rings identified a largely identical region showing similar effects to the one identified by the moving and stationary dots comparison. Because MT/MST, EBA, and LO overlapped in some subjects, we also repeated the analysis for voxels that were unique to each contrast (e.g., in MT/MST but not EBA or LO), and the results did not differ from the ones reported here for the full ROIs.

Random-effects analyses were performed for each ROI as follows. First, the fMRI time series was averaged for all voxels within a defined ROI in each subject. Except where noted in the results, this averaging occurred over all voxels in both hemispheres of an ROI. Next, a measure of the effect of interest (based on beta values for particular contrasts) was obtained from the general linear model for the spatially averaged ROI time series in each subject. Adaptation was quantified by calculating an adaptation ratio: $(\beta_{old} - \beta_{new})/(\beta_{old} + \beta_{new})$. Finally, these effects for each subject were either entered into a repeated measures analysis of variance (ANOVA) or, in the case of planned direct comparisons, paired *t* tests.

We also performed a whole-brain analysis as follows. For each individual subject, we derived unthresholded beta maps for the contrast of interest. Using a 12-parameter affine transformation with nonlinear deformations, we then normalized these maps into a standard coordinate space (MNI). We initially calculated normalization parameters by using each subject's high-resolution anatomical scan. After normalization, we spatially smoothed the maps with a kernel with full-width half-maximum of 8 mm. Finally, we conducted a random-effects analysis by testing whether the mean value across subjects in each voxel was significantly different from zero. For each contrast of interest, we used permutation methods to determine a cluster size threshold

for voxels significant at $p < .001$ (two-tailed, uncorrected) that corresponded to a corrected significance of $p < .05$ (Nichols & Holmes, 2002).

In our primary analysis, the voxelwise general linear model included four task covariates, one for each of the four different adaptation conditions, constructed by convolving delta functions aligned to onset of each movie with a subject- and task-specific estimate of the hemodynamic response. We fit three other statistical models in addition to the primary one. To test whether the adaptation effects we observed depended on transitivity, we fit a version of the primary model that split each of the four covariates modeling the different adaptation conditions according to whether the action involved was transitive or intransitive, for a total of eight covariates. To obtain the estimated responses presented in Figure 4, we fit a model that used a Fourier basis set (Ardekani & Kanno, 1998) to estimate the response in each of the four adaptation conditions. This model included seven covariates for each condition: one DC (mean) component, three sine components of different frequencies, and three cosine components of differ-

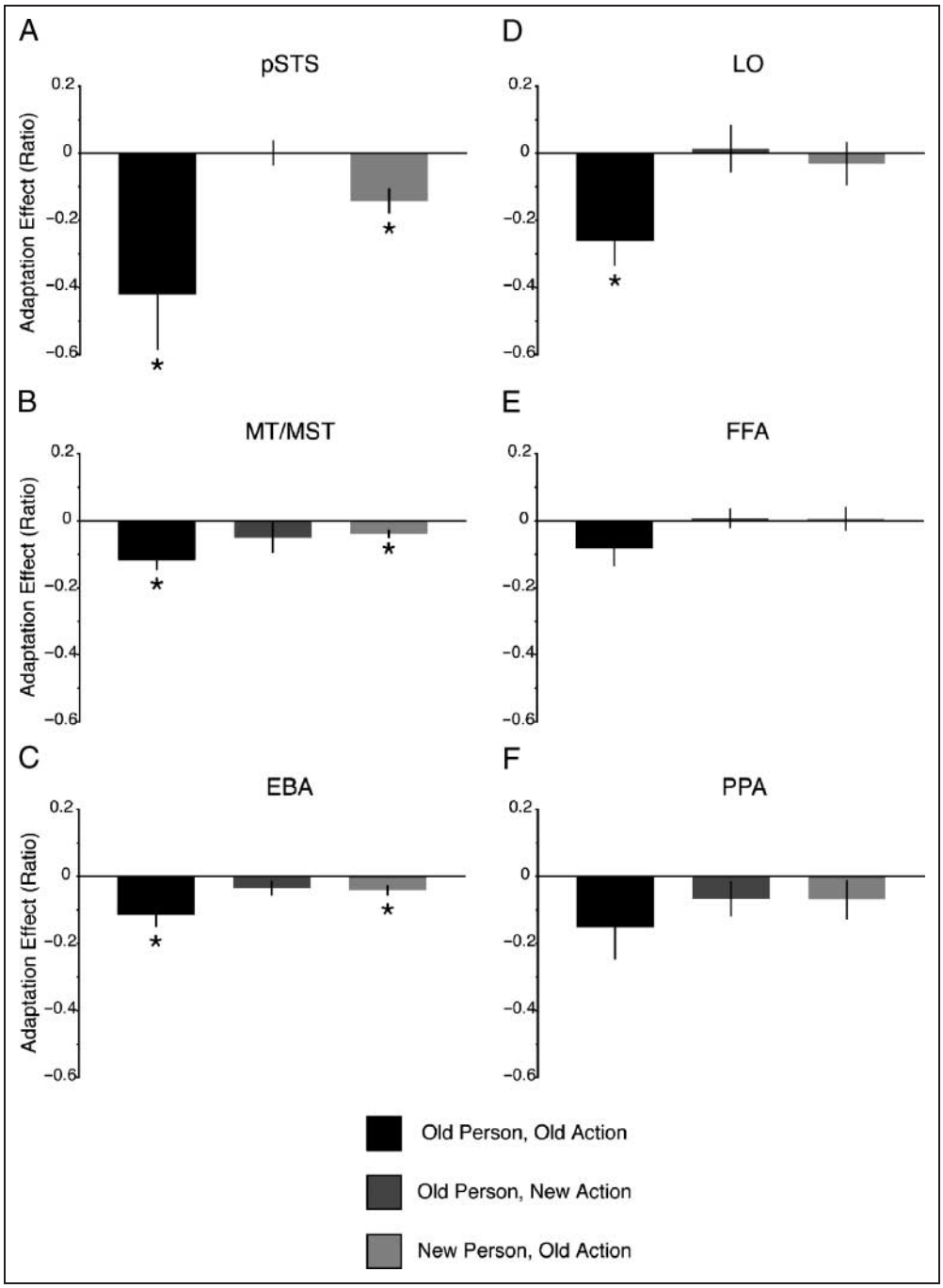


Figure 4. Neural adaptation effects in functional ROIs. Neural adapation effects are graphed for each condition in (A) pSTS, (B) MT/MST, (C) EBA, (D) LO, (E) FFA, and (F) PPA. Adaptation effects are expressed as a ratio: $(\beta_{old} - \beta_{new})/(\beta_{old} + \beta_{new})$. Error bars represent the standard error of the mean. Asterisks indicate an effect is significant at $p < .05$. All ROIs are bilateral.

Table 1. Behavioral Performance of fMRI Subjects

	Reaction Time (msec)	*% Responses < 2 sec*
Old Person, Old Action	926 ± 70	99.3 ± 0.5
Old Person, New Action	1224 ± 62	95.8 ± 1.5
New Person, Old Action	1050 ± 68	98.6 ± 0.8
New Person, New Action	1186 ± 64	97.2 ± 1.0

ent frequencies. The estimated response is then the sum of these seven fitted covariates. This model is an analog of a trial average, except in the frequency domain rather than the time domain; a trial average estimates the response at each point in time in the trial, whereas the Fourier model estimates the components of the response at different frequencies. We estimated the responses in each condition in this manner, rather than by calculating a trial average, because the beginning of each trial was jittered with respect to the image repetition time. To evaluate different potential mechanisms for the adaptation effects we observed, we were interested in whether the hemodynamic response peaked at different times in the different adaptation conditions. Our primary model assumed that the shape of the hemodynamic response, including the delay to peak of the response, was the same in each condition. Therefore, to address this question, we also fit a model that allowed the delay to peak to vary across conditions, based on the method developed by Henson, Price, Rugg, Turner, and Friston (2002) and Liao et al. (2002). This method involves fitting two covariates for each condition; the first (the canonical hemodynamic response) primarily fits the height of the response, and the second (the first derivative of the canonical hemodynamic response) primarily fits the delay to peak of the response. The beta values associated with these two covariates can then be used to estimate the delay to peak of the hemodynamic response for that condition.[1]

RESULTS

Behavioral Results

During scanning, subjects performed a speeded judgment for each movie indicating how often they typically see the action being performed (more/less than once a week). Response data indicated that subjects reliably performed the task. Subjects' responses agreed with the typical response (determined in a separate rating study) in 84 ± 2% of cases, and were consistent (same response given to different exemplars of the same action) in 90 ± 2% of cases.

Reaction time data from this task are reported in Table 1. A repeated measures ANOVA indicated a significant effect of condition on reaction time, $F(3,24) = 44.184$, $p < .0001$. Subjects demonstrated a robust repetition priming, as the Old Person, Old Action condition was significantly faster than all others (paired t test, all ps $< .0001$). Subjects also demonstrated an action-specific priming, with the New Person, Old Action condition being significantly faster than either of the New Action conditions (paired t test, both ps $< .001$). A repeated measures ANOVA also indicated a significant effect of condition on the percentage of responses within the 2-sec time limit, $F(3,24) = 5.021$, $p = .0077$. Specifically, subjects made more responses within the 2-sec time limit for the Old Person, Old Action condition compared to either of the New Action conditions (paired t test, both ps $<.05$).

ROI Analyses

For our primary analysis, we functionally identified six bilateral ROIs (see Figure 3). Table 2 provides information about the size of each ROI and the number of subjects for whom we identified each ROI. Within each

Table 2. Properties of Functional ROIs

	ROI Identified in (Fraction of Subjects)	*Includes Left Hemisphere in (Fraction of Subjects)*	*Size in Left Hemisphere (± SEM, Voxels)*	*Includes Right Hemisphere in (Fraction of Subjects)*	*Size in Right Hemisphere (± SEM, Voxels)*
pSTS	9/9	6/9	43 ± 19	9/9	51 ± 14
MT/MST	9/9	9/9	40 ± 5	9/9	58 ± 5
EBA	9/9	7/9	38 ± 12	9/9	75 ± 11
LO	8/9	8/9	44 ± 15	3/9	30 ± 6
FFA	8/9	7/9	14 ± 4	8/9	32 ± 8
PPA	9/9	9/9	60 ± 16	9/9	83 ± 19

subject, we averaged over all voxels in both hemispheres within each ROI and fit a general linear model to the spatially averaged time series. To test whether there were any effects of adaptation condition across subjects, the beta values from this model for each of the four adaptation conditions were entered into a repeated measures ANOVA with adaptation condition as a factor. There was a significant effect of adaptation condition in pSTS, $F(3,24) = 10.476$, $p = .0001$; MT/MST, $F(3,24) = 7.264$, $p = .0012$; EBA, $F(3,24) = 5.967$, $p = .0034$; and LO, $F(3,24) = 10.556$, $p = .0002$, but not in FFA, $F(3,21) = 2.205$, $p = .11$, or PPA, $F(3,24) = 2.870$, $p = .057$. To quantify the different adaptation effects, we calculated an adaptation ratio (AR) from the beta values as $(\beta_{old} - \beta_{new})/(\beta_{old} + \beta_{new})$. We calculated three ratios for repetition adaptation (Old Person, Old Action vs. New Person, New Action), action-specific adaptation (New Person, Old Action vs. New Person, New Action) and person-specific adaptation (Old Person, New Action vs. New Person, New Action).

In pSTS (Figures 4A and 5A), there was significant repetition adaptation, AR mean ± $SE = -.42 \pm .17$, $t(8) = -2.547$, $p = .034$, and significant action-specific adaptation, AR $= -.14 \pm .04$, $t(8) = -3.753$, $p = .0056$, but no significant person-specific adaptation (AR $= .00 \pm .04$). In addition, action-specific adaptation was reliably larger than person-specific adaptation in pSTS, $t(8) = -3.512$, $p = .0079$. Both MT/MST (Figures 4B and 5B) and EBA (Figures 4C and 5C) showed significant repetition adaptation, MT/MST: AR $= -.12 \pm .03$, $t(8) =$

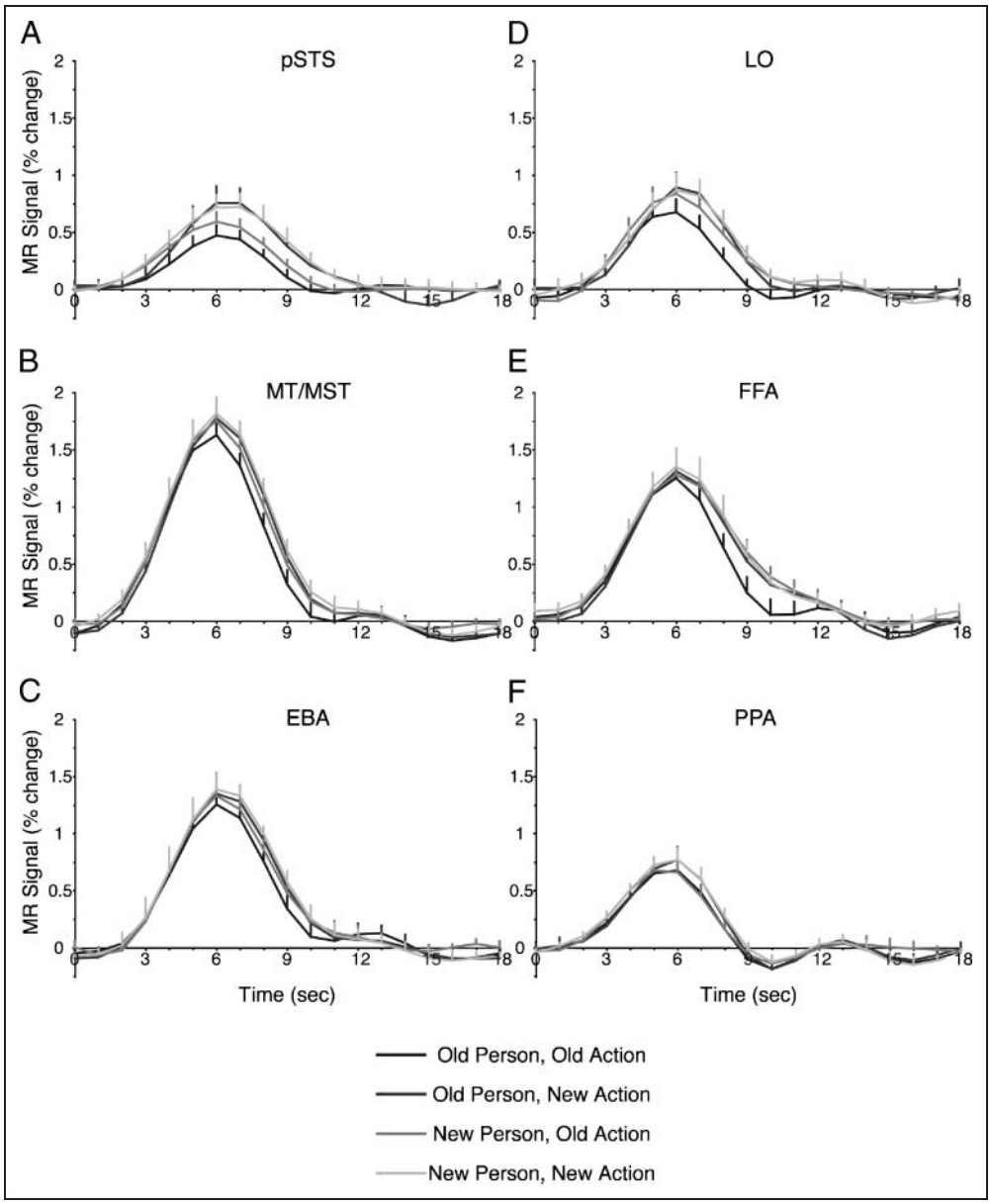


Figure 5. Estimated responses in functional ROIs. Mean estimated responses are graphed for each adaptation condition in: (A) pSTS, (B) MT/MST, (C) EBA, (D) LO, (E) FFA, and (F) PPA. Error bars represent the standard error of the mean, across subjects. Responses to each adaptation condition were estimated for an 18-sec window for each subject using an unbiased Fourier basis set (sine and cosine regressors at three frequencies plus one DC component). All ROIs are bilateral.

-4.258, $p = .0028$; EBA: AR $= -.12 \pm .03$, $t(8) = -3.435$, $p = .0089$, and significant action-specific adaptation, MT/MST: AR $= -.04 \pm .01$, $t(8) = -4.070$, $p = .0036$; EBA: AR $= -.04 \pm .01$, $t(8) = -3.155$, $p = .014$. However, although the person-specific adaptation effect did not reach significance in either MT/MST or EBA, MT/MST: AR $= -.05 \pm .04$, $t(8) = -1.156$, $p = .28$; EBA: AR $= -.03 \pm .02$, $t(8) = -1.753$, $p = .12$, it was also not reliably different from the action-specific effect (paired t test, both ps $> .5$). In LO (Figures 4D and 5D), only the repetition adaptation effect reached significance: repetition AR $= -.26 \pm .07$, $t(7) = -3.721$, $p = .0074$. FFA (Figures 4E and 5E) showed a similar pattern to LO, but the repetition adaptation effect failed to reach significance: repetition AR $= -.08 \pm .05$, $t(7) = -1.599$, $p = .15$. In contrast, none of the adaptation effects reached significance in PPA (Figures 4F and 5F) (all ps $> .10$). Finally, these various patterns of effects across the six ROIs were significantly different from each other. In an ANOVA with ROI and adaptation effect as factors, there was a significant interaction between ROI and adaptation effect, $F(10,60) = 2.365$, $p = .0197$.

As shown in Figure 1, half of the movies depicted intransitive actions that only involved movements of the body, whereas half depicted transitive actions that also involved objects. To test whether the adaptation effects we observed depended on transitivity, we fit an additional model that divided each of the four adaptation conditions according to whether they contained a transitive or intransitive action. In ANOVAs with transitivity and adaptation condition as factors, none of the ROIs showed a significant transitivity by adaptation condition interaction (F test, all ps $> .10$).

To test for hemispheric differences, we calculated adaptation ratios separately for the left- and right-hemispheric components of each ROI. In ANOVAs with hemisphere and adaptation effect as factors, none of the ROIs showed a significant hemisphere by adaptation effect interaction (F test, all ps $> .10$). Furthermore, a direct comparison of action-specific adaptation across hemispheres did not reach significance in pSTS, MT/MST, or EBA (paired t test, all ps $> .10$). However, although not significant, there was a trend for action-specific adaptation to be more reliable in the right hemisphere, pSTS: left AR $= -.02 \pm .09$, $t(5) = -.220$, $p = .83$, right AR $= -.21 \pm .05$, $t(8) = -4.222$, $p = .0029$; MT/MST: left AR $= -.04 \pm .03$, $t(8) = -1.687$, $p = .13$, right AR $= -.04 \pm .02$, $t(8) = -2.612$, $p = .031$; EBA: left AR $= -.01 \pm .02$, $t(6) = -.499$, $p = .64$, right AR $= -.05 \pm .01$, $t(8) = -3.318$, $p = .0106$.

Whole-brain Analysis

In addition to focused hypothesis testing in each ROI, we also performed a whole-brain analysis to detect large effects outside of these ROIs (see Figure 6 and Table 3). The left lateral occipitotemporal cortex showed both significant repetition adaptation (Old Person, Old Action < New Person, New Action), as well as action-specific adaptation (New Person, Old Action < New Person, New Action). In all cases, there was a bilateral effect in lateral occipitotemporal regions at slightly lower thresholds (see Figure 6). We also observed repetition adaptation bilaterally in the ventral occipitotemporal cortex, dorsolateral prefrontal cortex, and dorsomedial prefrontal cortex, and action-specific adaptation in the left ventral prefrontal and bilateral dorsomedial prefrontal cortex. Person-specific adaptation (Old Person, New Action < New Person, New Action) was seen in the ventromedial prefrontal cortex.

Is Neural Adaptation an Effect of Behavioral Priming?

The neural adaptation effects we observed in pSTS, MT/MST, and EBA largely correlated with the behavioral priming effects seen in the frequency judgment task (Old Person, Old Action < New Person, Old Action < Old Person, New Action = New Person, New Action). We expected such a correlation between neural activity (in areas involved in action recognition) and behavior (reaction time in the frequency judgment task) given that both measures should reflect improved efficiency of action recognition with repeated stimuli. However, one could argue that neural adaptation is an epiphenomenon of behavioral priming, simply reflecting a global ''shutting down'' of activity as subjects finish the task more quickly (Henson, 2003). The specificity in location of action-specific adaptation argues against this time-on-task account, which would predict widespread effects in all brain regions engaged by the stimuli. However, we performed an additional analysis to disconfirm this time-on-task account. This account, as well as some of the other proposed mechanisms for adaptation (Henson, 2003), predicts that the response peak should occur sooner in adapted conditions because adaptation would be caused by a decrease in the duration of neural activity. We tested whether the adaptation effects we observed were accompanied by a temporal shift in the response peak, using the method developed by Henson et al. (2002) and Liao et al. (2002) (see Methods). A significant shift in the peak response accompanied repetition adaptation (Old Person, Old Action vs. New Person, New Action) in MT/MST, $t(8) = -7.062$, $p = .0001$), EBA ($t(8) = -5.874$, $p = .0004$) and FFA ($t(7) = -2.872$, $p = .024$. Intriguingly, in all three cases, the size of this shift was similar to the 260-msec behavioral priming effect seen for the Old Person, Old Action condition (241 ± 34 msec in MT/MST, 223 ± 38 in EBA, and 285 ± 99 in FFA). Such a significant shift for the repetition effect was not found in pSTS, LOC,

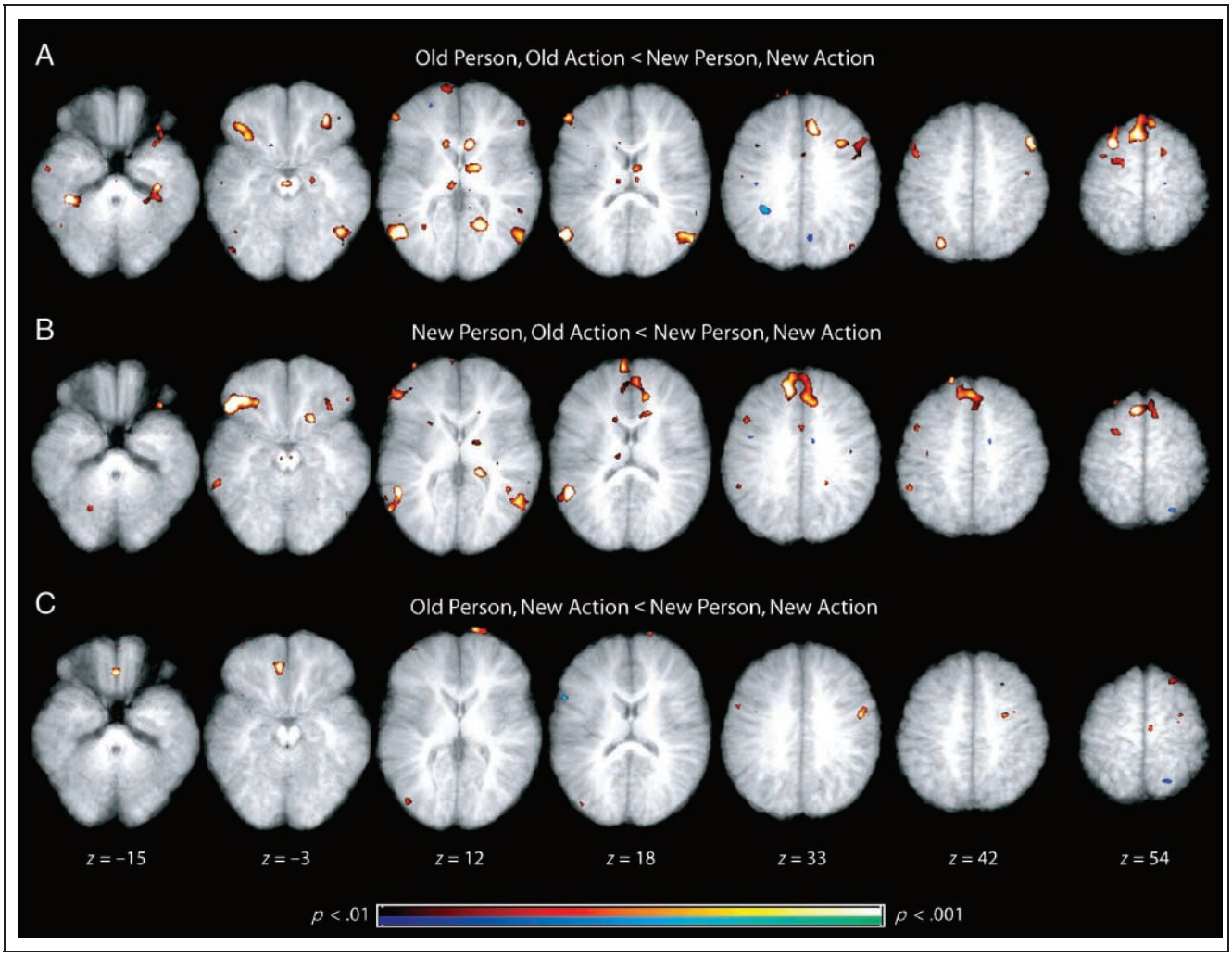


Figure 6. Neural adaptation effects across the whole brain. Displayed are the results of a whole-brain analysis for three contrasts: (A) Old Person, Old Action < New Person, New Action (repetition effect); (B) New Person, Old Action < New Person, New Action (action-specific effect); and (C) Old Person, New Action < New Person, New Action (person-specific effect). Activations are overlaid on the average of each subject's normalized brain. The color gradient goes from $p < .01$ to $p < .001$ (both two-tailed, uncorrected).

or PPA (paired t test, all ps $> .10$). More importantly, no significant shift was found in any ROI for the action-specific or person-specific effects (paired t test, all ps $> .30$).

DISCUSSION

We used repetition-related decreases in neural activity to probe the neural bases of action recognition. We found that pSTS, MT/MST, and EBA showed adaptation for stimuli in which the action was repeated but the person involved was not. Although previous studies have found increased activity in these regions when people see actions, our findings demonstrate that these three areas are sensitive to the *particular* action seen because the identity of the action alone (whether someone is dribbling or kicking) distinguishes repeated from novel actions. Such action-specific adaptation cannot be explained by sensitivity of these areas simply to the presence of motion or the human form. Thus, these results provide compelling evidence that these areas within the lateral occipitotemporal cortex play a critical role in action recognition.

Action recognition likely includes multiple stages, from the perceptual categorization of complex motion patterns to the conceptual understanding of the goal of an action or the intention of the agent (e.g., see the recent model in Giese & Poggio, 2003). Based on the known physiology of these regions (Jellema, Baker, Wicker, & Perrett, 2000; Andersen, 1997; Perrett et al., 1989), we suggest that adaptation in pSTS reflects action specificity at a more conceptual stage—involving similarities of goals or intentions across different exemplars of particular actions—whereas adaptation in MT/MST reflects action specificity in perceptual processing—

Table 3. Location of Significant Activations in Whole-brain Analysis

Anatomical Location of Cluster	*MNI Coordinates of Peak Voxel*	*Peak Voxel (z Value)*	*Cluster Size (Voxels)*
Repetition adaptation (Old Person, Old Action < New Person, New Action)			
L. ventral temporal	−39, −39, −18	3.86	11
Midbrain	0, −21, −9	3.97	7
R. medial prefrontal	15, 15, 3	4.26	19
R. ventral occipital	21, −60, 9	3.67	8
L. lateral occipitotemporal	−54, −72, 12	4.31	31
R. medial prefrontal	12, 24, 33	3.64	8
R. dorsolateral prefrontal	51, 15, 42	3.69	10
L. dorsolateral prefrontal	−24, 9, 51	4.16	12
L. medial prefrontal	−6, 18, 54	3.73	15
Action-specific adaptation (New Person, Old Action < New Person, New Action)			
L. ventral prefrontal	−45, 18, −3	4.71	48
L. lateral occipitotemporal	−48, −54, 12	4.51	16
R. medial prefrontal	9, 27, 27	3.80	11
L. medial prefrontal	−9, 36, 30	3.58	11
L. medial prefrontal	−6, 18, 54	4.09	17
Person-specific adaptation (Old Person, New Action < New Person, New Action)			
Ventromedial prefrontal	0, 24, −15	3.81	13

All activations significant at a cluster size threshold of $p < .05$ are reported. Permutation methods were used to determine a significant cluster size for voxels with $p < .001$ (two-tailed, uncorrected). This threshold was seven to nine voxels, depending on the contrast. L = left; R = right.

involving similarities in the motion patterns across different exemplars. Because the current experiment involved the activation of these representations during visual perception, we consider it an open question whether the same action-specific representations are also activated during motor planning (as suggested by the mirror neuron hypothesis; see Rizzolatti et al., 2001).

pSTS showed the greatest sensitivity and selectivity for repeated actions. The proportional decrease was largest in pSTS, and the action-specific effect in pSTS was reliably larger than the person-specific effect. Previous studies have shown that regions of the superior temporal sulcus show greater activity for moving compared to stationary bodies, for point-light biological motion compared to random-dot motion, or for moving bodies compared to moving objects (Beauchamp, Lee, Haxby, & Martin, 2002; Rizzolatti et al., 2001; Allison et al., 2000; Grossman et al., 2000; Decety & Grezes, 1999; Bonda et al., 1996; Howard et al., 1996). These findings could potentially be explained by the presence of biological motion or by the joint presence of motion and a biological form. Saxe, Xiao, Kovacs, Perrett, and Kanwisher (2004) found differences in activity in the superior temporal sulcus between conditions that were matched on the precise pattern of visible motion and concluded that this region responds to the perception of intentional action rather than biological motion alone. Our finding that pSTS shows action-specific adaptation demonstrates that neural activity in this region is not only sensitive to biological motion or intentional actions, but also distinguishes between different particular actions. Consistent with the idea that pSTS harbors conceptual representations of particular actions, this region also shows greater activity for action words (Kable et al., 2002, 2005), and lesions in this area impair conceptual knowledge about actions (Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003).

Although the effect was smaller, we also observed action-specific adaptation in MT/MST. Although MT/MST's role in motion processing is well known, the action-specific adaptation we report cannot be explained merely by the presence of motion because *all* of the movies contained motion. Nor can this effect be explained by repetition of the same *exact* pattern of

motion because different people naturally perform the same action in different manners. Nor can this effect be explained by repetition of a simple component of the motion pattern, such as overall direction, because in our stimuli the overall direction of motion does not distinguish between different actions (rightward motion does not distinguish between walking, marching, crawling, skipping, jumping, rolling, or cartwheeling). Rather, action-specific adaptation is best explained by similarities between different exemplars in a higher dimensional space that incorporates multiple components of the motion pattern. To our knowledge, this is the first demonstration that motion processing within MT/MST differentiates between particular actions. This sensitivity might explain activation in human MT/MST for static pictures of actions (Kable et al., 2002; Damasio et al., 2001; Kourtzi & Kanwisher, 2000).

EBA also exhibited action-specific adaptation. Although less is known about the response properties of this region, the initial report characterizing EBA hypothesized that it might be involved in the recognition of actions performed by human bodies (Downing et al., 2001). The finding that the EBA shows adaptation for repeated actions establishes that this region participates in action recognition, perhaps through an analysis of the body postures involved in different actions.

The pSTS, MT/MST, and EBA ROIs were all bilateral, and thus included voxels in both hemispheres in most subjects (Table 2). Action recognition impairments have been associated with left-hemisphere damage (Gainotti & Lemmo, 1976). In contrast, fMRI studies have generally found bilateral or right-lateralized activity when subjects view actions (Saxe et al., 2004; Kable et al., 2002; Grossman et al., 2000). We did not find conclusive evidence for hemispheric differences in action-specific adaptation. The pSTS, MT/MST, and EBA ROIs generally included more voxels from the right hemisphere (Table 2), and an analysis dividing these ROIs by hemisphere found a trend for greater action-specific adaptation in the right hemisphere. However, in the whole brain analysis, action-specific adaptation was stronger in the left lateral occipitotemporal cortex (Table 3 and Figure 6).

Our finding that some brain regions contain action representations that are abstracted away from the agents involved has important implications for cognitive development. Children consistently learn verbs after nouns, and the action referent for a verb is far less transparent than the object referent for a noun. Mandler (2004) suggests that the ability to abstract actions from the specific details of the individual objects involved may be required before a spatial event can be mapped onto language. Similarly, Gentner (2003) suggests that the recognition of actions as distinct from the agent is a central feature of ''why we're so smart,'' allowing a cognitive shift from conceptualizing concrete perceptual objects to conceptualizing more abstract relations among objects. The lateral occipitotemporal region containing pSTS, MT/MST, and EBA is well situated to integrate auditory input with motion information and social cues to establish verbal labels for actions. In addition, the lateral temporal cortex is one of the regions that matures last in the developing brain (Gogtay et al., 2004), suggesting that this region is engaged in relatively complex aspects of perceptual cognition.

Other Brain Regions

In contrast to our findings in pSTS, MT/MST, and EBA, we did not find action-specific or person-specific adaptation in LO, PPA, or FFA. We did find repetition adaptation in LO and a significantly earlier time to peak in FFA for the repetition condition. Because the action clips contain both people and objects, such repetition effects are consistent with previous findings of adaptation for faces or objects in the fusiform gyrus and LO (James et al., 2002; Vuilleumier et al., 2002; Koutstaal et al., 2001; Grill-Spector et al., 1999). Given FFA's role in face recognition, one might have expected person-specific adaptation in this area. However, in our stimuli, the whole body was visible and moving, so cues other than the face may have been more important in identifying the person.

We did, however, detect person-specific adaptation in the ventromedial prefrontal cortex in the whole-brain analysis. Our ability to detect such person-specific effects in at least one region strengthens the specificity of the action-specific effects we found in other regions. Person-specific activity in the ventromedial prefrontal cortex may reflect conceptual representations of individual people, as this region also shows greater activity when subjects name people compared to animals or tools (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004), and damage to this area produces profound deficits in social interaction (Eslinger & Damasio, 1985).

In the whole-brain analysis, we also detected action-specific adaptation in the ventrolateral and dorsomedial prefrontal cortex. Previous studies of the mirror neuron system in humans and monkeys have suggested a role for the ventrolateral prefrontal cortex in action recognition (Rizzolatti et al., 2001), and the action-specific responses we report are consistent with this role. However, we should also note that there are alternative explanations of these effects in terms of motor planning. Because the same action entailed the same motor response in our task, the effects in the ventrolateral and dorsomedial prefrontal cortex could reflect adaptation related to the selection or preparation of the task-related motor response (Dobbins et al., 2004). A related possibility is that subjects could have reflexively prepared the same action they were viewing, and the effects in the ventrolateral and dorsomedial prefrontal cortex reflect adaptation of this task-unrelated motor planning.

Perhaps surprisingly, the whole-brain analysis did not reveal action-specific adaptation in the inferior parietal cortex. Many previous studies have associated action recognition or action knowledge impairments with damage to the left inferior parietal cortex (Tranel et al., 2003; Varney & Damasio, 1987; Ferro, Martins, Mariano, & Caldas, 1983; Heilman, Rothi, & Valenstein, 1982). Although the role of the inferior parietal cortex is emphasized in these discussions, it should be noted that most impaired patients also have damage to the posterior superior and middle temporal gyrus (Varney & Damasio, 1987; Ferro et al., 1983; Heilman et al., 1982). However, even if the critical region for action recognition impairments is the inferior parietal cortex, there are three possible reasons why we did not see action-specific adaptation there. First, adaptation would not be seen if the critical role played by the inferior parietal cortex was similar for all actions and thus not action specific—for example, a general role of spatial and temporal processing in perceiving sequential movements. Second, the actions we studied did not focus on grasping and reaching, as is common in apraxia studies. A recent study that did find action-specific activity in the inferior parietal cortex (Shmuelof & Zohary, 2005) used actions involving different kinds of grasping motions, with only the hand and forearm of the actor visible. In contrast, the actions in our experiment mostly involved the whole body, and the agent's whole body was visible. Third, the inferior parietal cortex may specifically instantiate knowledge of the mechanical advantages afforded by tools, a knowledge domain not emphasized in our experiment.

Alternative Explanations for Adaptation Effects

In general, our conclusions are consistent with several proposed neuronal mechanisms for fMRI adaptation, such as decreased firing of all neurons responsive to the stimulus (Grill-Spector & Malach, 2001), the formation of sparser representations using fewer neurons (Wiggs & Martin, 1998), or more efficient access of preexisting representations (Henson, 2003). However, there are two other explanations for adaptation, based on attentional effects, which should be considered. Because these explanations undercut the logic of adaptation designs, they are a concern for all studies using this technique.

One alternative explanation is that adaptation is an attentional by-product of behavioral priming (Henson, 2003). The signal decreases we observed might reflect a decreased duration of neural activity simply because brain regions engaged by the stimuli shut down as the subject finishes the task earlier. For two reasons, such a time-on-task explanation could not account for action-specific adaptation in pSTS, MT/MST, and EBA. First, the pattern of adaptation differed significantly across the ROIs we examined, indicating that action-specific adaptation was not a general effect observed in all active regions. Similarly, in the whole-brain analysis, we failed to observe action-specific adaptation in many regions—such as the primary visual cortex—that were active during the action movies. Second, the time-on-task explanation is predicated on signal decreases from a decreased duration of neural activity, which would have an earlier hemodynamic response peak. However, we detected no significant change in the time to peak associated with action-specific adaptation.

A related but distinct explanation is that adaptation directly reflects nonspecific attentional processing. pSTS, MT/MST, and EBA might be involved in the general deployment of attention, and thus show decreased activity during those conditions that subjects finish more quickly. However, such an attentional explanation is not consistent with previous findings because it predicts that pSTS, MT/MST, and EBA should show adaptation for *any* condition associated with behavioral priming. When subjects attend to object identity, they exhibit behavioral priming for different views or different exemplars of previously seen objects, yet lateral occipitotemporal areas do not exhibit object-specific adaptation under these circumstances. Rather, object-specific adaptation is observed in the ventral occipitotemporal cortex (James et al., 2002; Vuilleumier et al., 2002; Koutstaal et al., 2001).

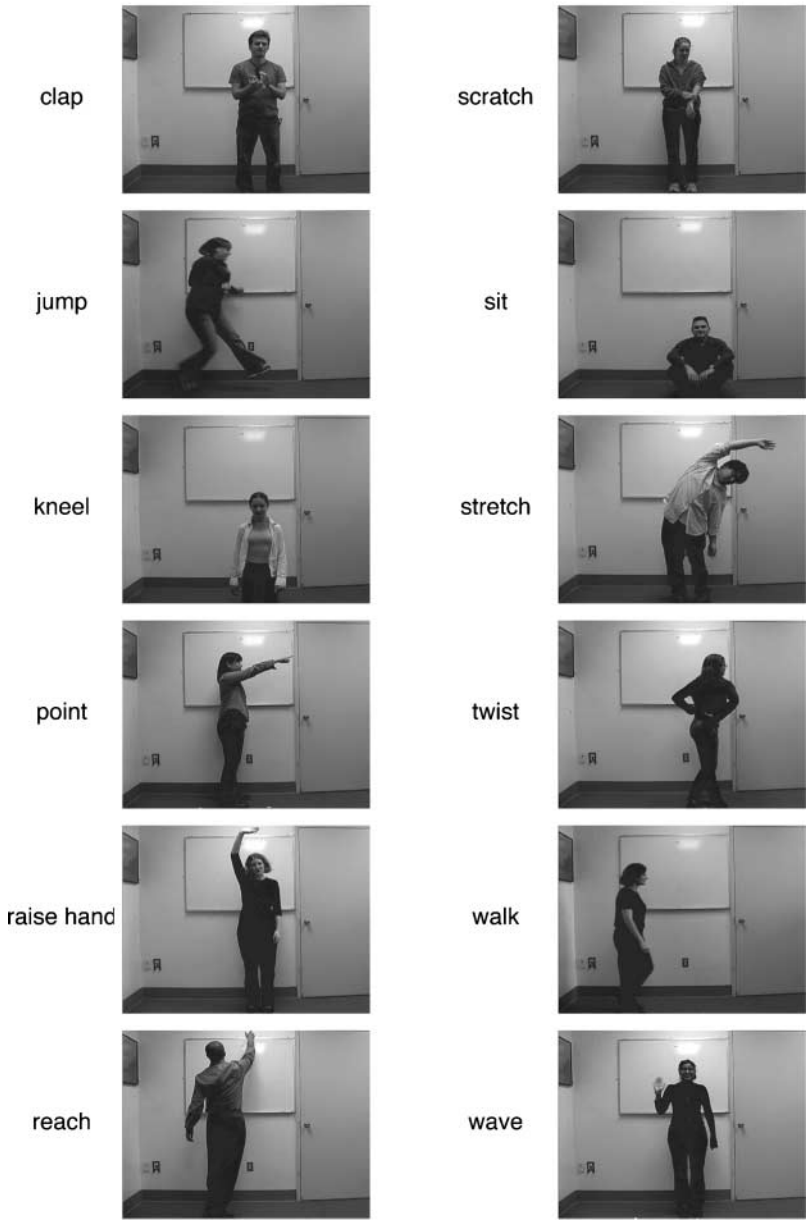
Conclusion

In conclusion, we have demonstrated that three areas within the lateral occipitotemporal cortex—pSTS, MT/MST, and EBA—are involved in action recognition, and that the sensitivity of these areas is more complex than hitherto considered. Given that actions involve changes in the relationship between objects in space, it is not surprising that these areas are located in an intermediate position on the cortical surface between more dorsal parietal areas involved in spatial processing and more ventral occipitotemporal areas involved in object recognition. Consistent with anatomical evidence (Boussaoud, Ungerleider, & Desimone, 1990), these results suggest the existence of a ''ventrodorsal'' or ''lateral'' stream of visual processing, including the classical dorsal stream areas MT and MST, which is important for action recognition.

Appendix

Example of the actions and persons used as stimuli are provided. Each of the 48 different actions and 48 different people are represented, and the examples are categorized according to whether the action was transitive/intransitive and common/uncommon. Only a single frame from the full movie is shown. While these frames are shown in grayscale, the movie were presented to the subjects in color.

Intransitive, Common



Intransitive, Uncommon

bow

march

cartwheel

punch

crawl

roll

elbow

salute

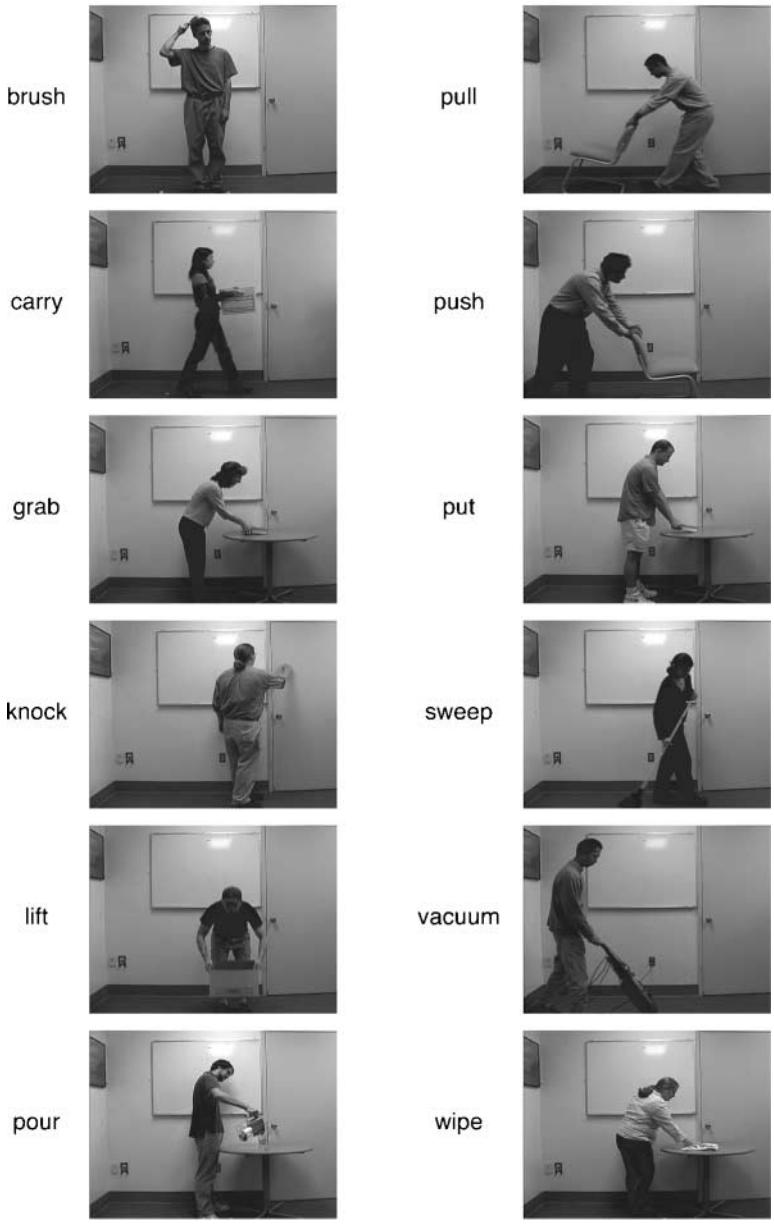
jumping jack

skip

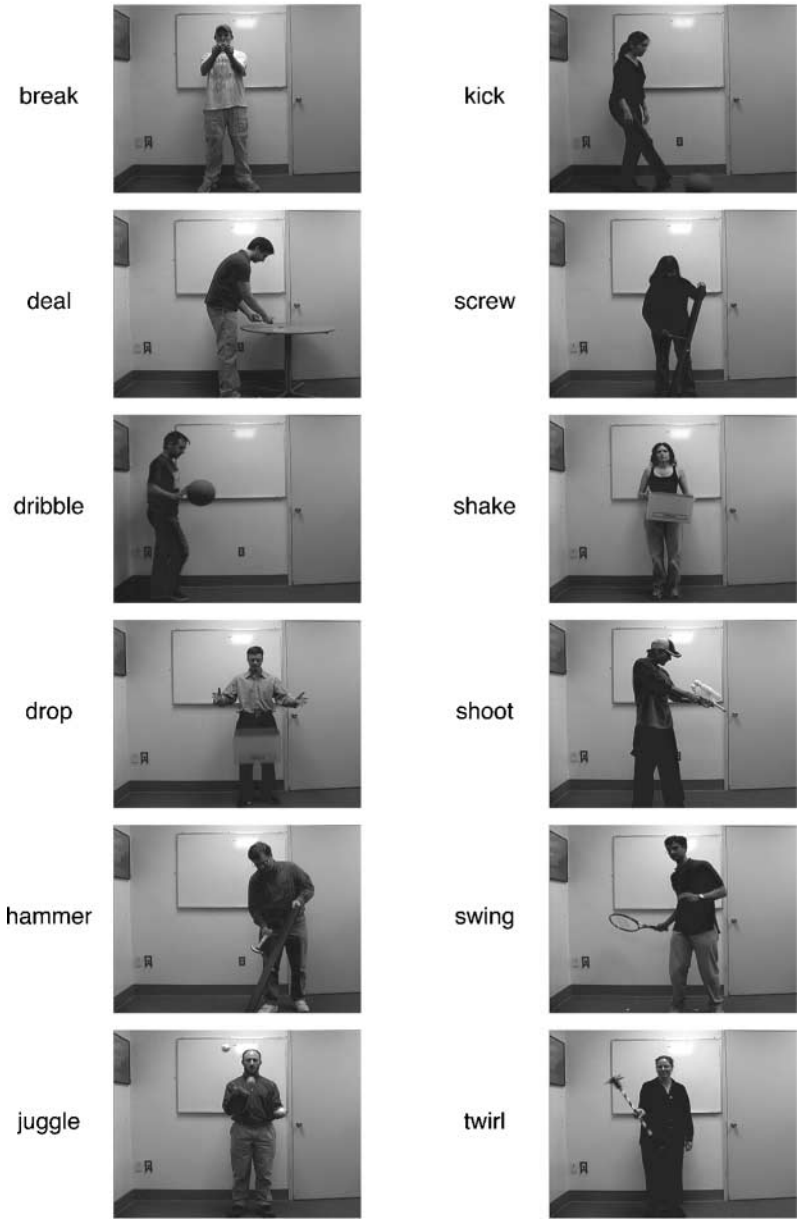
kick

stomp

Transitive, Common



Transitive, Uncommon



Acknowledgments

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Note

1. In the place of the canonical hemodynamic response and its first derivative, we used the first and second eigenvectors from an analysis of the variability in hemodynamic responses in a large group of subjects (Aguirre et al., 1998). The first eigenvector is similar in shape to the canonical hemodynamic response, and the second eigenvector primarily shifts this response in time, just like the first derivative. This necessitated using a slightly different formula from the one provided by Henson et al. (2002) to calculate the time to peak of the response. The formula used was: peak (sec) = $2.2295 - (2 \times 2.2295)/(1 + e^{1.7737 \times \beta(\text{second eigenvector})/\beta(\text{first eigenvector})})$.

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