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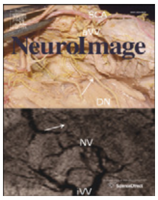

Squeezing lemons in the bathroom: Contextual information modulates action recognition

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ABSTRACT

Most every day actions take place in domestic rooms that are specific for certain classes of actions. Contextual information derived from domestic settings may therefore influence the efficiency of action recognition. The present studies investigated whether action recognition is modulated by compatibility of the context an action is embedded in. To this end, subjects watched video clips of actions performed in compatible, incompatible, and neutral contexts. Recognition was significantly slower when actions took place in an incompatible as compared to a compatible or a neutral context (Experiment 1). Functional MRI revealed increased activation for incompatible context in Brodmann Areas (BA) 44, 45, and 47 of the left ventrolateral prefrontal cortex (vlPFC; Experiment 2). Results suggest that contextual information - even when task-irrelevant - informs a high processing level of action analysis. In particular, the functional profiles assigned to these prefrontal regions suggest that contextual information activates associated action representations as a function of (in-)compatibility. Thus, incompatibility effects may reflect the attempt to resolve the conflict between action and context by embedding the presented action step into an overarching action that is again compatible with the provided context.

Introduction

Our daily activities take place in highly specialized places and rooms that are optimized for specific actions: In kitchens we prepare food, in bathrooms we engage in body care, but usually not vice versa. Since domestic settings are reminiscent of certain classes of actions, one may expect them to modulate the recognition of observed actions as well. Compatible contextual settings should constrain expectation in a facilitatory way, whereas incompatible ones should mislead expectation and thus cause interference. Its high relevance in real life notwithstanding, the influence of contextual information derived from domestic settings on action recognition has not been explored yet.

Action recognition has been defined as matching percepts of an action onto corresponding action stored in semantic memory (Jeannerod, 2006). According to Hamilton and Grafton (2007) actions can be described at three broad, hierarchically organized levels: the *muscle* level describes the pattern of muscle activity required for action execution, the *kinematic* level describes the characteristic movements of involved effectors in space and time, and the *goal* level describes the overarching desired outcome of the action. Contextual information may affect the perception–memory matching level of action recognition by activating contextually related action memories and thereby modulating the matching process via spreading activation in the semantic network (Neely, 1977). In a similar vein, contextual information may affect higher levels of action analysis, e.g. inference of (long-term) goals and prediction of subsequent motor acts.

In the present experiments, both behavioral as well as neuroimaging methods were employed to investigate whether contextual information provided by domestic settings affects action recognition, and if so, at which level of action analysis.

In a behavioral study (Experiment 1), it was tested whether compatibility of context and action affects the speed of action recognition. We then used fMRI (Experiment 2) to identify brain regions that are modulated by contextual compatibility, and therewith to elucidate which level of action analysis is affected by contextual compatibility. We expected early steps of action analysis to be reflected in the occipitotemporal cortex (Beauchamp et al., 2002; Hamilton and Grafton, 2007; Jastorff and Orban, 2009; Jastorff et al., 2009; Kable and Chatterjee, 2006) whereas inference of (long-term) goals and prediction of forthcoming motor acts to draw on prefrontal cortex as well as premotor–parietal loops (Iacoboni et al., 2005; Johnson-Frey et al., 2003; Kilner et al., 2007; Schubotz, 2007; Van Overwalle and Baetens, 2009; van Schie et al., 2006). Moreover, visual processing of rooms and places involves especially the parahippocampal place area (PPA; Epstein and Kanwisher, 1998). In monkeys, the parahippocampal cortex is connected to ventrolateral prefrontal, parietal and occipitotemporal cortices

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(Schmahmann and Pandya, 2006; Schmahmann et al., 2007), making these regions likely candidates for the interaction of contextual and action information.

In both experiments, subjects watched video clips of context-specific everyday actions performed in domestic settings that were either compatible or incompatible with the action. In addition, we employed a neutral condition where actions were performed in settings without any interior. According to our approach, a video clip was contextually "neutral" when it did not provide a clear bias as to which room it pertains, and therefore could not serve as a cue for contextual affiliation. Importantly, the neutral condition provided a baseline for evaluating facilitatory effects of the compatible and interference effects of the incompatible condition: Compatible but neither incompatible nor neutral contexts should bias action-relevant information and thereby facilitate action recognition. Similarly, incompatible but neither compatible nor neutral contexts should activate action-irrelevant information that interferes with the observed action.

In the behavioral study (Experiment 1), subjects were instructed to observe the action videos and to interrupt them by button press as soon as they recognized the presented action. We expected differences in the speed of recognition between the incompatible, the compatible, and the neutral condition: Facilitatory effects would manifest in faster responses to the compatible condition as compared to the incompatible and neutral conditions because contextual associations of the domestic setting should *pre-activate the representation of* the observed action (Bar, 2007). In contrast, interference effects would manifest in delayed responses for the incompatible condition as compared to the compatible and to the neutral condition. In this case, action recognition is hampered by pre-activation of incompatible action information that conflicts with the observed action.

In the fMRI Experiment, we tested whether, and if so, on which level, contextual information affects the neural signatures of action perception. As elaborated above, contextual modulation of the low/perceptual level was expected to be signified by occipitotemporal activation. Modulation of the high/goal inference level was expected to be signified by prefrontal and/or premotor activation.

To this end, a different group of subjects observed the same set of actions that were presented in the behavioral study. To ensure that subjects paid attention to the videos, they occasionally had to confirm or reject an action description with respect to the preceding trial.

Influences of contextual compatibility on action observation were assessed using conjunction analyses: facilitatory effects would be signified by decreases of neural activity in the conjunction (compatible vs. neutral) ∩ (compatible vs. incompatible), given that context-triggered pre-activation of the target action results in neural adaptation (Bedny et al., 2008; Gold et al., 2006; Henson, 2003). Similarly, interference effects would be signified by increases of neural activity in the conjunction (incompatible vs. neutral) ∩ (incompatible vs. compatible) due to *activation of irrelevant, potentially conflicting information* (Bedny et al., 2008; Cardillo et al., 2004). In order to determine the functional specificity of contextual (in-)compatibility for action perception, we furthermore analyzed whether putative activation sensitive to contextual compatibility overlapped with regions sensitive to action recognition. Regions involved in action perception were identified by contrasting actions in the neutral context with a resting baseline.

Moreover, incompatibility between context and action *was* expected to *trigger a* perceptual *re*-analysis of the domestic settings *in a top-down manner after incompatibility of context and action has been detected*. In that case, the BOLD response should increase in scene processing regions, especially the PPA. The PPA as well as other context-specific regions (i.e. retrosplenial cortex (RSC) and transverse occipital sulcus (TOS)) was identified using a separate functional localizer for places and scenes (Epstein and Kanwisher, 1998). We also included a functional localizer for body parts to identify the extrastriate body area (Downing et al., 2001), and for objects to identify the lateral occipital complex (Grill-Spector et al., 2001). This was done because both functional regions are located in the occipitotemporal cortex, which was part of our anatomical hypotheses (see Methods and Supplementary material for details).

All of the employed actions involved objects that were themselves also either compatible or incompatible to the context. To dissociate action-context compatibility from object-context compatibility effects, we additionally employed pantomime actions as a control. Pantomime actions used action-incompatible objects that were either context-compatible or not. Accordingly, object-context incompatible vs. object-context compatible pantomime should reveal effects of object incompatibility, if present, as well. If, in contrast, (in-)compatibility effects would be observed only for actions, but not for pantomime, these effects could not be ascribed to object-context (in-)compatibility, but unambiguously to action-context (in-)compatibility.

Methods

Behavioral experiment

Subjects

Forty-nine healthy volunteers (19–28 years, mean 23.7 years, 31 females, 2 left-handed) participated in the study. Three subjects did not enter the analysis because of poor performance (error rates higher than 2 standard deviations). All participants had normal or corrected-to-normal vision. Participants gave written consent before the experiment. Data were handled anonymously.

Stimuli

Thirty context-specific actions (e.g. using a stapler, cracking an egg, sawing a plank) were filmed in compatible, incompatible, and neutral contexts. Actions were object manipulations specific for the contexts "office", "kitchen" and "workshop" (see appendix). Each context was specified by the background, the working surface, and 3–5 context-specific stationary objects (e.g. computer screen, coffee machine, grinding machine). The neutral context was constructed by stretching a white sheet on a table forming a uniform surface without any corners. In each context, actions were filmed from an allocentric perspective (60° to the left of the actress) providing a convenient view on the object manipulation and the contextual setting (Fig. 1). Each video had a length of 3 s, a presentation rate of 25 frames per second and a display width and height of 720 × 576 pixels.

The actions started with grasping of the objects about 680 ms after video onset. Care was taken that the three action versions were performed in exactly the same manner for each of the three experimental conditions (see Supplementary material for examples in which the three action versions are displayed simultaneously).

To ensure (1) context-specificity and (2) context-incompatibility in the incompatible condition, a pilot study was performed where an independent group of subjects delivered a judgment on a Likert rating scale from 1 (very unlikely) to 6 (very likely), indicating how likely they found the presented actions for the particular contexts. All actions scored significantly higher for compatible than for incompatible contexts. The same Likert rating was employed in a post-experiment survey following the fMRI session (see Results).

Design and procedure

Subjects were seated approximately 60 cm away from a computer screen and next to the experimenter. Trials started self-paced by pressing a target button with the right index finger, followed by a short fixation phase (500 ms blank screen, 500 ms fixation cross at the center of the screen). Videos appeared at the center of the screen (subtending approximately 13.6 × 10.5° of visual angle). Subjects were instructed to press the target button as soon as they recognized the presented action. After button press, the video was replaced by a question mark at the center of the screen, and subjects had to name the recognized action. The verbal response was recorded using a built-in program of the

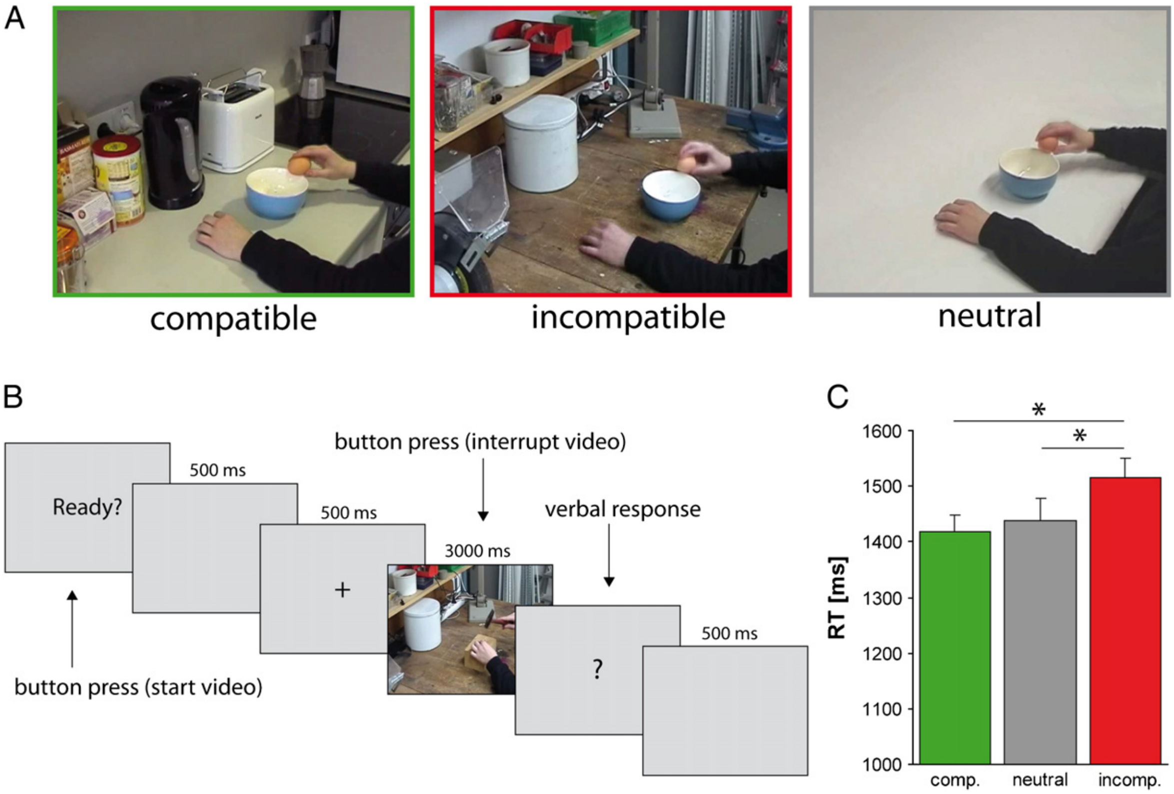

Fig. 1. (A) Experimental conditions for both Exp. 1 and 2 employed video clips of 30 actions (see Appendix) performed in compatible, incompatible, and neutral contexts. (B) Trial design of the behavioral experiment (Exp. 1). Subjects were instructed to press a button as soon as they recognized a presented action. After button press the video was replaced by a question mark requesting subjects to verbally indicate the recognized action. (C) Results of Exp. 1. Subjects were significantly slower in recognizing actions embedded in incompatible as opposed to compatible and neutral contexts. Error bars indicate standard error of mean.

presentation software (Presentation 13.1, Neurobehavioral Systems). The experimenter indicated by button press not visible to the subject whether the response was correct or not. Only correctly answered trials with RTs shorter than 3000 ms entered the statistical analysis. The trial ended with a blank screen for 500 ms.

Each subject watched each of the 30 actions only once during the experiment (10 trials per condition). Stimuli were hence balanced across three groups of subjects (n = 15, 15, 16). The occurrence of contexts was balanced within subjects so that each subject saw each of the three domestic settings 6–7 times and the neutral setting 10 times. The trial order was pseudorandomized, so that transitions of contexts and transitions of conditions occurred equally often; i.e., for each subject (= 30 trials) each of the 16 possible transitions between the 4 contextual settings occurred 1–2 times, and each of the 9 possible transitions between the 3 conditions occurred 3–4 times.

FMRI experiment

Subjects

Eighteen healthy volunteers (21–29 years, mean 24.9 years, 12 females) were enrolled in the fMRI experiment. Subjects were right-handed according to the Edinburgh Inventory Manual Preference (Oldfield, 1971). All participants had normal or corrected-to-normal vision, and were native German speakers. No participant had a history of neurologic or psychiatric disorder. Participants gave written consent before fMRI measurement. The experimental standards were approved by the local ethics committee of the Medical Faculty, University of Cologne, Germany. Data were handled anonymously.

Stimuli and task

Stimuli of the behavioral experiment were used. Subjects were presented with 30 trials per condition, ensuring that any within-subject differences between conditions could not be attributed to idiosyncrasies of the actions. In addition to the conditions of the behavioral experiment we also employed additional conditions with pantomime actions (i.e. actions performed with action-incompatible objects; Schubotz and von Cramon, 2009). Pantomime actions were either compatible or incompatible with the context and involved objects that were also either compatible or incompatible with the context.

In the present study, pantomime actions served to control for putative object-context effects. We hence contrasted (1) object-context incompatible with object-context compatible trials when actions were compatible to the context, and (2) object-context incompatible with object-context compatible trials when actions were compatible to the context. In a third contrast (3), we collapsed action-compatible and action-incompatible trials. The resulting two conditions were pantomime actions involving context-compatible objects and pantomime actions involving context-incompatible objects, irrespective of action-context compatibility.

Subjects were instructed to observe the presented actions. They were informed that some of trials (20%) were followed by a verbal action description (question trial). Question trials were employed to ensure that subjects paid attention to the actions. Because questions occurred well after presentation of the action clips, they were not expected to yield significant performance differences between conditions. Subjects had to indicate by button press whether the description matched or did not match the action of the preceding trial (n-1). The description matched the action in 50% of the question trials. Every second question trial was followed by an empty trial in which subjects were instructed to fixate a small square in the center of the screen providing a resting baseline.

All trials had a length of 6 s, starting with a variable jitter (0, 500, 1000, or 1500 ms) to enhance the temporal resolution of the BOLD

Table 1
Peaks of activation in the direct contrasts.

Area		BA	*x*	*y*	*z*	*Z*	mm³
Incompatible vs. compatible							
L	Precentral gyrus (sup. PMv)	6	−35	6	36	2.94	3078
L	IFG/IFS	44	−44	9	18	3.47	l.m.
L		44	−41	21	18	2.93	l.m.
L	IFG	45	−41	27	6	2.92	l.m.
L	IFG	47	−35	24	0	3.09	l.m.
Incompatible vs. neutral							
L	IFG/IFS	44/45	−44	24	21	3.50	3105
L	IFG	47	−32	21	3	3.16	l.m.
L	PHC	35/36/37	−29	−51	0	4.42	14310
L	Cuneus/Fusiform gyrus	37	−23	−78	0	4.41	l.m.
R	PHC	35/36/37	22	−48	0	4.59	29646
R	Cuneus/Lingual gyrus	17/18	7	−84	0	6.69	l.m.
R	TOS	18/19	28	−78	27	3.18	l.m.
R	Thalamus, Pulvinar		22	−27	0	3.21	l.m.
Compatible vs. neutral							
L	PHC	35/36/37	−26	−51	0	4.85	2025
L	Cuneus/Lingual gyrus	17/18	−23	−78	0	4.40	11664
R	PHC	35/36/37	25	−45	0	4.68	32373
R	Cuneus/Lingual gyrus	17/18	10	−84	3	7.20	l.m.
R	Thalamus, Pulvinar		16	−28	0	3.40	l.m.

Hemisphere (L, R), Macroanatomical specification, Brodmann area (BA), Talairach coordinates (*x*, *y*, *z*), maximal *Z* scores (*Z*), and cluster volumes (mm³); *z*-thresholded at 2.576, corrected cluster threshold $p<.05$. Abbreviations: IFG inferior frontal gyrus, IFS inferior frontal sulcus, PHC parahippocampal cortex, sup. PMv superior ventral premotor cortex, TOS transversal occipital sulcus.

response. Videos and verbal action descriptions were followed by a fixation square until the next trial started.

The order of conditions per action was balanced across subjects to rule out habituation effects with respect to the actions. The trial order was pseudorandomized to equate transition probabilities between contexts and transition probabilities between conditions. Furthermore, the occurrence of question trials and baseline trials was balanced so that in each condition, there were the same numbers of trials preceded and followed by question and baseline trials.

Functional localizers

Following the main experiment, a functional localizer experiment adapted from Downing et al. (2006) was conducted: subjects viewed images from 4 categories in 16 blocks (4 blocks per category, randomized block order) with a length of 17 s, separated by a fixation screen for 8 s.

Categories were: places (indoor and outdoor), body parts (hands, arms, legs, face parts, torso), objects (tools and household articles), and scrambled objects (24×24 pixels). 40 full-color 720×576-pixel images per category were used; each image was presented twice in the experiment. Within each block, 20 images were presented for 300 ms; with an inter-stimulus-interval (ISI) of 650 ms. Subjects were instructed to indicate via button press with the right index finger when two identical images were presented in direct succession (one-back task, 1 or 2 repetitions per block).

Table 2
Peaks of activation for compatibility and incompatibility of context and action.

Area		BA	*x*	*y*	*z*	*Z*	mm³
Conjunction (compatible vs. incompatible) ∩ (compatible vs. neutral)							
L	IFG	47	−41	30	3	−2.49	1107
L	posterior MTG	37	−47	−57	6	−2.30	1026
R		37	37	−51	−6	−2.59	2808
*Conjunction (incompatible vs. compatible) ∩ (incompatible vs. neutral)**							
L	IFG/IFS	44/45	−41	15	21	2.94	1296
L	IFG	47	−32	21	0	2.68	81

Hemisphere (L, R), Macroanatomical specification, Brodmann area (BA), Talairach coordinates (*x*, *y*, *z*), maximal *Z* scores (*Z*), and cluster volumes (mm³). Abbreviations: IFG inferior frontal gyrus, IFS inferior frontal sulcus, MTG middle temporal gyrus. **z*-thresholded at 2.576, corrected cluster threshold $p<.05$.

Table 3
Functional localizers for actions, places, body parts, and objects.

Area		BA	*x*	*y*	*z*	*Z*	mm³
Actions in neutral context vs. fixation baseline							
L	IFG/IFS	44/45	−38	33	21	4.29	104382
L	Precentral gyrus (sup. PMv)	6	−50	0	36	5.76	l.m.
L	Precentral gyrus (PMd)	6	−20	0	51	5.95	l.m.
L	anterior IPS	7	−53	−24	42	6.35	l.m.
L	posterior IPS	7	−26	−54	54	6.17	l.m.
L	occipito-temporal cortex	37/19	−40	−67	3	7.44	l.m.
R	IFG/IFS	44/45	40	30	15	4.29	86562
R	Precentral gyrus (sup. PMv)	6	40	9	24	5.76	l.m.
R	Precentral gyrus (PMd)	6	31	−3	57	6.04	l.m.
R	anterior IPS	7	28	−36	51	6.25	l.m.
R	posterior IPS	7	19	−51	57	6.33	l.m.
R	occipito-temporal cortex	37/19	37	−60	3	8.08	l.m.
L	SMA	6	1	−3	57	5.32	675
L	Thalamus (Pulvinar)		−20	−30	6	5.33	1620
R			16	−27	6	5.34	1944
L	cerebellum (VIIb/VIIIa)		−29	−54	−42	6.40	6183
R			16	−54	−39	6.55	5589
Places vs. objects, body parts							
L	PHC (PPA)	35/36/37	−26	−45	−3	6.86	20412
L	RSC	26/29/30	−17	−57	21	5.86	l.m.
L	TOS	18/19	−23	−87	24	5.92	l.m.
R	PHC (PPA)	35/36/37	22	−42	−3	7.77	24543
R	RSC	26/29/30	10	−51	18	6.62	l.m.
R	TOS	18/19	10	−93	21	6.41	l.m.
Body parts vs. objects							
L	posterior MTG (EBA)	37/39/19	−50	−63	15	6.63	10206
L			46	−60	6	6.59	15147
L	Fusiform gyrus	37	40	−48	−9	4.38	l.m.
L	posterior IPS	7	−32	−42	54	5.49	19926
R	anterior IPS	7	−47	−24	39	4.83	l.m.
R	Precentral gyrus (PMd)	6	−23	−3	48	4.60	l.m.
R	Precentral gyrus (sup. PMv)	6	−50	12	30	4.62	l.m.
R	posterior IPS	7	31	−30	45	5.67	15822
	anterior IPS	7	46	−24	42	4.54	l.m.
Objects vs scrambled objects							
L	posterior MTG (LO)	37/19	−50	−69	12	6.68	32967
L	TOS	18/19	−41	−75	30	4.99	l.m.
L	Fusiform gyrus/PHC (pFs)	37	−32	−39	−9	6.37	l.m.
R	posterior MTG (LO)	37/19	37	−72	9	6.73	32562
R	Fusiform gyrus/PHC (pFs)	36	25	−45	−3	5.94	l.m.

Hemisphere (L, R), Macroanatomical specification, Brodmann area (BA), Talairach coordinates (*x*, *y*, *z*), maximal *Z* scores (*Z*), and cluster volumes (mm³); *z*-thresholded at 2.576, corrected cluster threshold $p<.05$. Abbreviations: EBA extrastriate body area, IFG inferior frontal gyrus, IFS inferior frontal sulcus, IPS intraparietal sulcus, LO lateral occipital cortex, MTG middle temporal gyrus, pFs posterior fusiform gyrus, PHC parahippocampal cortex, PPA parahippocampal place area, PMd dorsal premotor cortex, PMv ventral premotor cortex, TOS transversal occipital sulcus.

MRI data acquisition

After instruction and a short practice of the main task (not the localizers' task) outside the scanner, subjects were placed supine on the scanner bed with the right index or middle finger positioned on the response buttons. They were provided with earplugs and headphones to attenuate scanner noise. Form-fitting cushions were used to prevent arm and head motion.

The experiment was performed in a 3-T Siemens Trio system (Erlangen, Germany) using a standard birdcage head coil. 26 axial slices (192 mm field of view; 64×64 pixel matrix; 4 mm thickness; 1 mm spacing; in-plane resolution of 3×3 mm) covering the whole brain were acquired using a single-shot gradient EPI sequence (2000 ms repetition time; 30 ms echo time; 90° flip angle; 116 kHz acquisition bandwidth) sensitive to BOLD contrast. Functional imaging (90 images per condition of the main experiment, 32 images per category of the localizer experiment) was followed by acquisition of 26 anatomical T1-

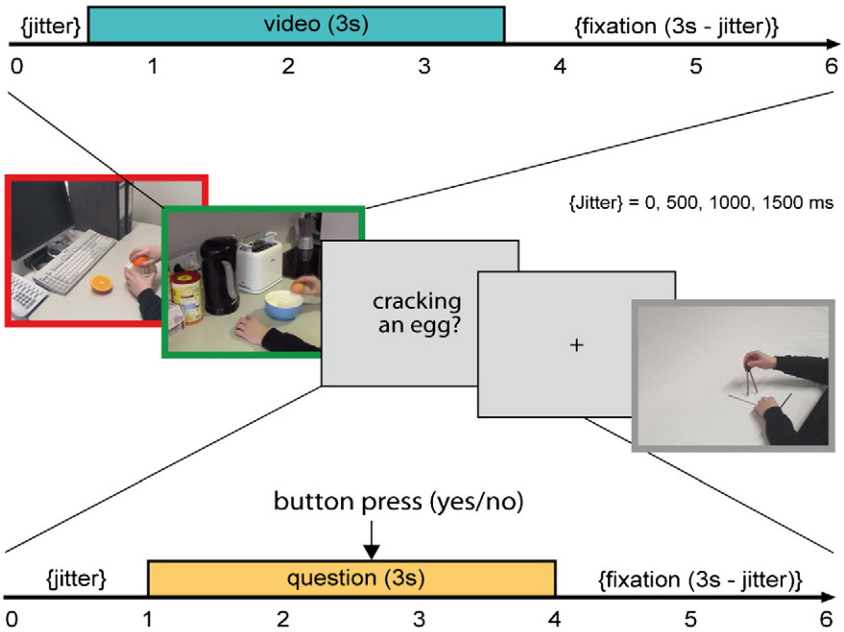

Fig. 2. Event-related design of the fMRI experiment (Exp. 2). Action videos were presented intermixed with verbal action descriptions (question trials, 20% of action trials). Subjects were instructed to attend to the videos and recognize the actions. In question trials subjects had to indicate per button press whether an action description matched the preceding action (50%) or not (50%).

weighted MDEFT images (Norris, 2000). In a separate session, high resolution whole-brain images were acquired from each subject using a T1-weighted 3-D-segmented MDEFT sequence.

MRI data analysis

fMRI data were processed using the software package LIPSIA 1.5.0 (Lohmann et al., 2001). An offline motion-correction was performed with the Siemens motion-correction protocol PACE (Siemens, Erlangen, Germany). A cubic-spline interpolation was employed to correct for the temporal offset between slices acquired in one image. A temporal high-pass filter with a cut-off frequency of 1/80 Hz was used. Spatial smoothing was performed with a Gaussian filter of 5.65 mm FWHM. To align the functional data slices with a 3-D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (three rotational, three translational) was performed. An optimal match between the 3-D individual dataset and the EPI-T1 slices was achieved by using the rotational and translational parameters acquired on the basis of the MDEFT and the EPI-T1 slices. The MDEFT volume dataset with 160 slices and 1 mm slice thickness was standardized to the Talairach stereotactic space (Talairach and Tournoux, 1988). Rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system, thus generating output data with a spatial resolution of $3 \times 3 \times 3$ mm (27 mm^3). The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1995; Worsley and Friston, 1995). For the main experiment the design matrix was generated with a gamma function, convolved with the hemodynamic response function. Brain activations were analyzed time-locked to onset of the movies, and the analyzed epoch comprised the full duration (3 s) of the presented movies, the duration of the null events (6 s) and the reaction time in question trials (max. 3 s), respectively. Analyzed epochs of the localizer experiment comprised the duration of blocks (17 s) and were convolved with a Gaussian function. The model equation, including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to account for the temporal autocorrelation (Worsley and Friston, 1995). In the following, contrast images, i.e. beta value estimates of the raw-score differences between specified conditions, were generated for each participant. As all individual functional datasets were aligned to the same stereotactic reference space, the single-subject contrast images were entered into a second-level random effects analysis for each of the contrasts.

One-sample *t* tests were employed for the group analyses across the contrast images of all subjects that indicated whether observed differences between conditions were significantly distinct from zero. The *t* values were subsequently transformed into *Z* scores.

To correct for false-positive results, in a first step, an initial voxelwise *z*-threshold was set to $z = 2.576$ ($p = 0.005$). In a second step, the results were corrected for multiple comparisons using cluster-size and cluster-value thresholds obtained by Monte Carlo simulations at a significance level of $p = 0.05$, i.e. the reported activations are significantly activated at $p < .05$, corrected for multiple comparisons at the cluster level.

Conjunctions were calculated by extracting the minimum *Z* value of the two input contrasts for each voxel (Nichols et al., 2005).

Results

Behavioral experiment

Behavioral effects were considered significant at an α level of 0.05. Mean reaction times (RTs) were calculated for all conditions and each subject. Results are reported in Fig. 1. A repeated measures ANOVA indicated a significant effect of condition on RT ($F_{(2,\ 90)} = 4.39$, $p = 0.015$). RTs were significantly slower for the incompatible condition (mean ± standard error of mean, 1515 ± 34 ms) compared to the compatible (1418 ± 30 ms; one-tailed paired *t* test, $t_{45} = 3.64$, $p < 0.001$) and neutral condition (1438 ± 41 ms; one-tailed paired *t* test, $t_{45} = 3.64$, $p = 0.021$). RTs between neutral and compatible condition did not differ significantly (one-tailed paired *t* test, $t_{45} = -0.5$, $p = 0.31$).

No significant effects were found for error rates (compatible: $6.0 \pm 1.1\%$, incompatible: $3.8 \pm 0.9\%$, neutral: $2.9 \pm 0.8\%$; repeated measures ANOVA: $F_{(2,\ 90)} = 2.30$, $p = 0.106$).

After the experiment, subjects were asked whether they noticed anything or anything odd in the videos. Only 26% (12 of 46 subjects) spontaneously recognized that some actions were performed in action-incompatible contexts.

FMRI experiment

Behavioral performance

Behavioral performance was assessed by analyzing responses to question trials. These referred to details of the object manipulation, not to contextual compatibility. Question trials were implemented to control for subjects' attention to the actions. Overall error rates were low (compatible: 3.3 ± 1.8%, incompatible: 0.8 ± 0.8%, neutral: 2.8 ± 1.9%), ensuring that subjects paid attention to the presented actions. Differences between conditions were not significant (repeated measures ANOVA: $F_{(2,\ 34)} = 0.65$, $p = 0.528$).

Following the fMRI session, subjects evaluated the likelihood of each action to take place in each context. The Likert scale ranged from 1 (very unlikely) to 6 (very likely). Overall, context-compatible trials scored significantly higher (mean ± standard deviation, 5.88 ± 0.25) than context-incompatible trials (2.19 ± 0.81; paired-samples *t*-test: $t_{17} = 34.17$, $p < 0.001$, one-tailed), corroborating our stimulus manipulation. Importantly, using the rating scores as regression coefficients in a parametric fMRI design yielded activation identical to the contrast incompatible vs. compatible context (see section below).

fMRI effects of incompatibility

Interference effects were hypothesized to manifest as increases of BOLD response in the incompatible as compared to the compatible and the neutral condition. Contrasting incompatible with compatible contexts revealed activation maxima in the left vlPFC (inferior frontal gyrus, IFG, and lower bank of inferior frontal sulcus, IFS) and the superior ventral premotor cortex (PMv, Fig. 2). A similar activation in the left vlPFC was also found in the contrast incompatible vs. neutral context (Fig. 2, Table 1). Further activation was found in inferior temporal cortex and parahippocampal gyri (PHG), and occipital regions including cuneus, lingual gyrus, and transverse occipital sulcus. These activations reflect different amounts of visual/contextual information in (in-)compatible vs. neutral contexts (cf. Supplementary material for a detailed discussion and ROI analysis).

No significant activation was found in the reverse contrast. The conjunction of both contrasts [(incompatible vs. compatible) ∩ (incompatible vs. neutral)] confirmed the effect of incompatibility in the left vlPFC (Fig. 3).

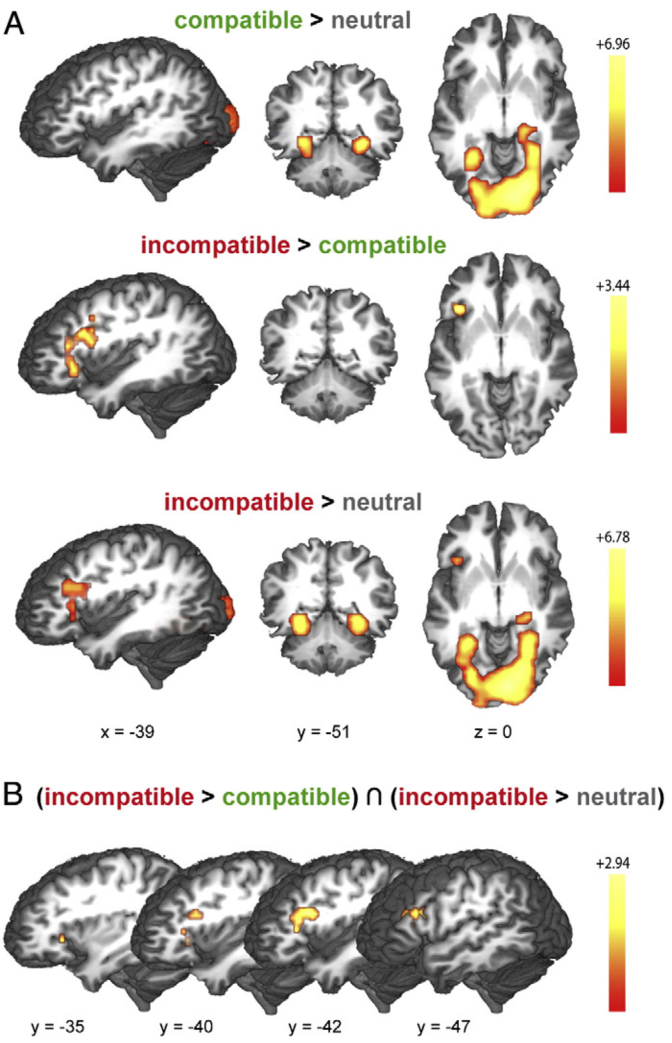

Fig. 3. Results of Exp. 2. (A) Direct contrasts between experimental conditions. (B) A conjunction analysis revealed activation specific for compatibility and incompatibility of context and action. Conjunction of the contrasts (incompatible vs. compatible context) ∩ (incompatible vs. neutral context) revealed increased responses for incompatible contexts in the left vlPFC (BA, 44/45 and BA 47), *z*-thresholded at 2.576, corrected cluster threshold p = 0.05.

fMRI effects of compatibility

Facilitatory effects were hypothesized to manifest as decreases of BOLD response in the compatible as compared to the incompatible and the neutral condition. The conjunction [(compatible vs. incompatible) ∩ (compatible vs. neutral)] yielded a common overlap in the left IFG (BA 47) and in the occipitotemporal lobe bilaterally. The activations, however, were relatively weak (see Table 2). Even after lowering the significance level of the multiple comparisons corrections ($z = 1.96$), activations fell below the statistical threshold. Activations will hence not be discussed further.

Overlap of compatibility effects with regions sensitive to action recognition

To test whether regions sensitive to contextual compatibility of context and action overlap with regions sensitive to action recognition in general we computed the contrast actions in the neutral context vs. resting baseline (Table 3). We then tested whether there is an overlap with the conjunction (incompatible vs. compatible) ∩ (incompatible vs. neutral). Contrasting actions in the neutral context vs. rest yielded activation of dorsal and superior ventral premotor cortex, bilateral supplementary motor area, bilateral ventrolateral prefrontal cortex, left intraparietal sulcus, bilateral posterior occipitotemporal cortex, and right cerebellum. Activations overlapped with compatibility effects in left dorsal BA 44 (44d) and the posterior part of BA 45 (45p) but neither in the anterior part of BA 45 (45a; Amunts et al., 2010) nor in BA 47 (Fig. 4).

FMRI effects object-context incompatibility

Since all actions involved objects, (in-)compatibility effects could in principle also arise before the action unfolds due to object-context (in-)compatibility. As a control, we contrasted object-context incompatible vs. object-context compatible trials in pantomime. This was done in three steps of analysis: (1) object-context incompatible vs. object-context compatible trials when actions were compatible to the context, (2) object-context incompatible vs. object-context compatible trials when actions were compatible to the context, and (3) object-context incompatible vs. object-context compatible trials irrespective of action-context (in-)compatibility (i.e. contrasts (1) and (2) were collapsed in a conjunction).

In neither case, there was increased activation for object-context incompatible trials.

Discussion

The present behavioral and fMRI experiments were carried out to investigate whether action recognition is modulated by contextual information derived from domestic settings. To this end, subjects watched context-specific everyday actions taking place in compatible, incompatible, and neutral contexts. The behavioral experiment revealed that subjects recognized actions significantly faster when they took place in a compatible than in an incompatible context. However, since recognition was also faster in neutral than in incompatible contexts, but not faster in compatible than in the neutral context, findings point to an interference effect of incompatible contexts, not to facilitatory effects of compatible ones. In accordance to this result, the fMRI experiment yielded evidence for interference effects. Increased activation was recorded for incompatibility in the left ventrolateral prefrontal cortex (vlPFC). Activation overlapped with regions sensitive to action perception in dorsal BA 44 and the posterior part of BA 45 but not in the anterior part of BA 45 and BA 47, pointing to a network extension in case of action-context conflict. There was no significant common decreasing activity in compatible as compared to either neutral or incompatible contexts, and hence no evidence in favor of facilitatory neural mechanisms.

Together, results suggest that incompatible settings exert interference on action recognition/analysis. In particular, activation of vlPFC in the fMRI experiment indicates that interference affected not the perceptual analysis of action properties but rather higher levels of action interpretation, i.e. the inference of hierarchically superordinate action structures, as will be discussed hereafter.

Slower responses to actions in incompatible contexts

In the behavioral experiment, reaction times reflected how long subjects needed to recognize the presented action. When actions were performed in an incompatible context, subjects were about 100 ms slower than for compatible contexts, and about 80 ms slower when compared to the neutral context. Interestingly, compatible contexts did not substantially facilitate action recognition, but incompatible ones interfered with it.

Knowledge of and thus habituation to a compatible context may have caused reduced usage of contextual information in compatible trials, resulting in reaction times comparable to the neutral trials. Alternatively, the absence of facilitatory effects may be due to behavioral ceiling effects. Thus, actions were always so easy to recognize that compatible settings could not further improve or accelerate their recognition. Another reason for the absence of facilitatory effects may be that background objects in the compatible and incompatible conditions might have distracted attention from the action. The lack of background in the neutral context might thus have positively affected the subjects' responses. Indeed, isolated objects are recognized more easily than objects embedded in a compatible context (Boyce et al., 1989; Davenport and Potter, 2004; Murphy and Wisniewski, 1989). We hence cannot rule out that putative facilitatory effects of compatible contexts were masked/compensated by lower perceptual demands of neutral contexts. A possibility to overcome the problem of low-level perceptual differences between the neutral and the domestic settings could be to use a “scrambled” background in the neutral condition, providing the identical amount of visual information as the domestic settings. In addition, to account for mid-level perceptual differences (e.g. figure-ground segmentation, surface extraction, detection of contours and shapes, etc.) and recognition of background objects one would have to embed non-contextual (e.g. abstract) objects into the background. However, a background adjusted that way might be considered as unnatural and therefore evoke interference for that reason as well. Hence, interpretation and use of such a control condition would remain unclear. The choice of the appropriate background in a baseline condition is a generally unsolved problem that hampers a flawless differentiation between facilitation and interference in studies on visual scene effects (cf. Bar, 2004).

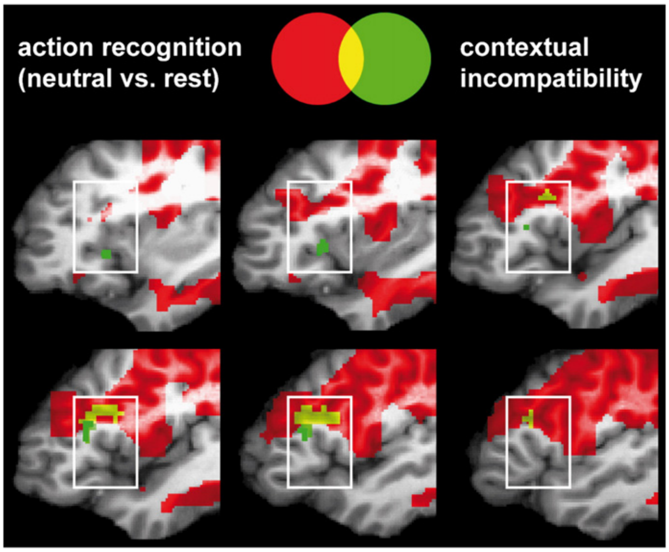

Fig. 4. Regions sensitive to contextual compatibility (green) overlap with regions sensitive to action recognition (red). The overlap was computed by superimposing the conjunction (incompatible vs. neutral) ∩ (incompatible vs. compatible) with the contrast actions in neutral settings vs. rest; *z*-thresholded at 2.576, corrected cluster threshold p = 0.05.

Neural effects of incompatibility

Observation of actions taking place in incompatible contexts as compared to either compatible or neutral ones increased activation in the left vlPFC, including BA 44/45 and BA 47. No significant effects were found in occipitotemporal regions, suggesting that recognition of perceptual properties of the action were not affected by contextual information. Likewise, contextual (in-) compatibility did not affect PPA activity, which was strongly activated by both action-compatible and action-incompatible contexts (cf. Supplementary material). In contrast, activation of the vlPFC rather suggests that contextual information influenced a high processing level during action analysis, for instance one relating to the inference of long-term goals. Dorsal BA 44 and posterior BA 45, but not BA 47 and anterior BA 45, overlapped with regions sensitive to action perception in general. This dissociation is in line with meta-analyses on action observation revealing involvement of BA 44 and BA 45 but not BA 47 (Caspers et al., 2010; Grezes and Decety, 2001; Van Overwalle and Baetens, 2009), and cytoarchitectonic studies that suggest a segregation of dorsal and ventral BA 44, and anterior and posterior BA 45 (Amunts et al., 2010).

Single-cell recordings in monkeys (Murata et al., 1997; Rizzolatti et al., 1988) as well as functional imaging (Rizzolatti and Craighero, 2004) and neuropsychological studies in humans (Buxbaum and Kalenine, 2010) suggest that left BA 44 of the vlPFC is involved in structuring sequences to realize particular outcomes (Fiebach and Schubotz, 2006; Grafman, 2002). During action perception, the same process may be exploited to generate top-down expectations about upcoming actions steps (Csibra, 2007; Fagg and Arbib, 1998; Friston et al., 2011; Schubotz and von Cramon, 2009). Here, contextual cues may modulate the concatenation of motor acts that are most likely to follow next. Indeed, observation of action seems to not only activate representations of the concurrent action but also of semantically related actions (Fogassi et al., 2005; Iacoboni et al., 2005). An imaging study where grasping objects in different situational contexts implied different actions to follow (grasping to drink or grasping to clean) engaged right BA 44 (Iacoboni et al., 2005). Related to this observation, we found that subjects, when asked to verbally indicate the actions in the behavioral experiment, they sometimes indicated not the actually presented action step, but rather a corresponding overarching action goal; i.e., they said “making pancake” instead of “cracking an egg”.

The activation of associated action representations may be a function of the probability of a given action to occur in a defined sequence. In terms of computations, domestic settings may shift the probability weights between semantically related action representations. For instance, observing someone squeezing a lemon triggers action memories that are likely to precede (halving the lemon) and to follow (pouring juice, preparing a drink, etc.). The likelihood of related actions to follow is equal in the compatible and in the neutral condition, because the latter does not negatively modulate the (high) probability weights between observed and the related, implied actions or action steps. In contrast, in order to make sense of “squeezing a lemon in the bathroom”, alternative logically related actions compatible with both the action and the contextual setting are searched for, resulting in the inference of the underlying intention: Maybe in this case, the actor wants to decalcify the tap. This mechanism offers an explanation of how context-driven modulation of associative strengths between actions might contribute to long-term goal inference. Since prediction of subsequent action steps depends on knowledge about long-term goals, currently perceived action steps are probably embedded into the most likely action sequence. Activation of BA 44 and 45p overlapped with activation for actions in neutral settings vs. rest, in line with according literature (Caspers et al., 2010; Grezes and Decety, 2001; Van Overwalle and Baetens, 2009). This finding hence supports the assumptions that concatenation of events is involved in action perception in general (Caspers et al., 2010; Schubotz and von Cramon, 2004). In contrast, BA 47 and 45a may only be required when additional resources are needed. Thus, to resolve context-action incompatibility, alternative action goals need to be found or generated, charging retrieval and selection of (semantic or episodic) memory. BA 47 has been shown to play an important role in the controlled access to stored conceptual representations, whereas BA 45 is activated for the selection among competitively activated representations (Badre et al., 2005; Gold et al., 2006; Moss et al., 2005). In our study, BA 47 could be required for the controlled retrieval of semantic information that is necessary to come up with plausible solutions (“What can be done with lemon juice in the bathroom?”). Anterior BA 45 may operate after retrieval to select appropriate action representations that accounts best for both the observed action and action representations triggered by the incompatible setting. Interestingly, when subjects actively contemplated about the likelihood to find actions in incompatible contexts, ratings were relatively moderate, i.e. they rarely judged context-incompatible actions as “very unlikely” (see scores of the post-session rating in the Results section). This observation suggests that subjects had a bias toward – and were quite successful in – finding plausible alternative long-term goals.

In summary, enhancement of activation in BA 44, 45 and 47 by contextual incompatibility points to enhanced memory search and the attempt to overcome the discrepancy by a plausible overarching action goal. We therefore suggest that RT differences measured in our behavioral experiment most probably evolved from processing stages where the perceptual properties of an action were already recognized and the activated representation in semantic memory conflicts with context-activated action representations on the goal level. An electrophysiological study on the effects of settings on object recognition measured earliest context compatibility effects around 300 ms after stimulus onset and the morphology and time course of the event-related potential resembled the N400 congruity signal typically observed in semantic context paradigms (Ganis and Kutas, 2003). We hence suggest that visual context information does not measurably affect action recognition before respective semantic information is activated, at least when actions are very easy to recognize.

Limitations

The task we employed required subjects to focus their attention on the action. Still, it is principally possible that interference effects arose by object-context incompatibility. In this case, effects of incompatibility should have been observed in the control pantomime actions as well. However, this was not the case. We hence can conclude that reported incompatibility effects were exclusively driven by action-context incompatibility.

With respect to the behavioral experiment, we cannot exclude object-context effects. Since actions unfold in time, however, one may argue that facilitated object recognition would not substantially interact with action recognition. This is because objects can be recognized within 150 ms (Thorpe et al., 1996) and responses to object recognition typically occur around 600 ms after stimulus onset (Ganis and Kutas, 2003; Thorpe et al., 1996). In our experiment, actions began about 680 ms after video onset, i.e., well after objects were recognized, and responses occurred after about 1400 ms after movie onset. Thus, when our actions started to unfold, objects most likely were already recognized in both compatible and incompatible contexts. Putative facilitated object recognition which may have occurred in our experiment is therefore unlikely to substantially contribute to the effects measured in the behavioral experiment.

Further experiments are needed to unambiguously test whether action-context incompatibility delays the inference of action goals, e.g. when no object information is available.

Concluding remarks

To sum up, domestic settings – although actually ignorable in our experiments – affected action recognition. This was revealed by slower recognition (Experiment 1) and by increased neural activity in the left ventrolateral prefrontal cortex (Experiment 2) when actions took place in incompatible settings. Effects are suggested to reflect interference between the currently observed action and actions implied by the incompatible setting. Increased neural responses likely reflect the embedding of the observed action into a logically possible action sequence (BA 44); this requires the retrieval of overarching action goals that are compatible with both the observed action and the action-incompatible setting (BA 47), and the selection among these alternatives in order to solve the experimentally induced conflict in the best-possible way (BA 45).

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2011.08.038.

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Appendix

List of employed actions and means (with standard deviations) of rating scores obtained in a post-session survey of the fMRI experiment. Subjects were asked for the likelihood to observe actions in the compatible and the incompatible setting. Ratings were from 1 (very unlikely) to 6 (very likely).

Action	Compatible	Incompatible
Whisking	5.72 ± 1.18	1.28 ± 0.46
Buttering a bread	6.0 ± 0.0	2.0 ± 1.08
Cracking an egg	6.0 ± 0.0	1.94 ± 1.0
Peeling a potato	6.0 ± 0.0	1.0 ± 0.0
Slicing a carrot	6.0 ± 0.0	1.17 ± 0.38
Squeezing a lemon	5.94 ± 0.24	2.06 ± 1.35
Grating cheese	5.83 ± 0.38	1.28 ± 0.67
Opening a bottle	5.67 ± 1.19	4.0 ± 1.03
Drying dishes	6.0 ± 0.0	2.56 ± 1.29

Appendix (*continued*)

Action	Compatible	Incompatible
Opening a can	6.0 ± 0.0	2.28 ± 1.18
Drawing a line with a ruler	5.44 ± 0.62	4.56 ± 1.34
Using a compass	5.0 ± 1.03	4.5 ± 0.86
Sharpening a pencil	5.61 ± 1.20	4.50 ± 1.29
Erasing	5.83 ± 0.38	4.33 ± 1.14
Sticking a stamp on a letter	6.0 ± 0.0	1.11 ± 0.32
Opening a letter with paper knife	5.94 ± 0.24	3.39 ± 1.82
Unlocking a cash box	4.28 ± 1.45	2.89 ± 1.57
Stamping	5.89 ± 0.32	2.0 ± 1.28
Hole-punching	6.0 ± 0.0	2.17 ± 1.38
Stapling sheets	5.72 ± 0.96	2.17 ± 1.54
Sawing	6.0 ± 0.0	1.0 ± 0.0
Screwing with screwdriver	5.94 ± 0.24	2.0 ± 0.97
Hammering nails	5.94 ± 0.24	1.94 ± 1.06
Planing wood	5.89 ± 0.32	1.0 ± 0.0
Painting	5.44 ± 0.98	2.06 ± 1.06
Rasping wood	5.89 ± 0.32	1.17 ± 0.51
Pulling out nail	5.89 ± 0.47	1.72 ± 0.67
Removing isolation of wire	5.8 ± 0.38	2.06 ± 1.06
Screwing with wrench	5.89 ± 0.32	2.28 ± 0.96
Isolating wire	5.67 ± 0.59	1.78 ± 1.0

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