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Brain activity for visual judgment of lifted weight



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ABSTRACT

It is well established that humans can recognize high-level aspects from point-light biological motion, such as gender and mood. If the task is to judge the manipulated weight we expected that sensorimotor regions should be recruited in the brain. Moreover, we have recently shown that chronic pain in a limb that is involved in the presented movement disturbs the weight judgment. We therefore hypothesized that some cortical regions usually activated during the processing of pain will also be activated while viewing point-light biological motion with the instruction to judge the manipulated weights. We investigated point-light biological motion of two types of movements performed with different weights in a blocked fMRI experiment in healthy subjects. In line with our a priori hypothesis, we found strong activity in the regions known as the neuromatrix of pain, such as the anterior cingulate (ACC), insula, as well as primary and secondary somatosensory regions. We also found activation in the occipital and temporal regions that are typical for biological motion, as well as regions in the cerebellum and prefrontal cortex. The activation of the somatosensory regions probably serves the judgment of the biological motion stimuli. Activation of the anterior cingulate and the insula might be explained by their role in the integration of behaviorally relevant information. Alternatively, these structures are known to be involved in the processing of nociceptive information and pain. So it seems possible that the interference between judgment of weights and perception of pain in chronic pain patients occurs in the somatosensory areas, anterior cingulate and/or insula. This finding provides important information as to the underlying mechanisms used for the weight judgment task, but also why chronic pain interferes with this task.

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1. Introduction

Point-light biological motion is a highly impoverished visual display of human movements (Johansson, 1973). Interestingly, this kind of stimuli are easily recognized in such detail that naive observers spontaneously report how many people are displayed and what each of them does. In an experimental setup subjects can judge the weight of an object that is manipulated by the actor in the point-light display (Runeson & Frykholm, 1981). Since this early study the weight-judging task has been used frequently, especially because it provides an interesting link between the visual and the sensorimotor systems (Alaerts, Swinnen, & Wenderoth, 2010; Auvray, Hoellinger, Hanneton, & Roby-Brami, 2011; Bingham, 1987; Bosbach, Cole, Prinz, & Knoblich, 2005; de Lussanet et al., 2012; Hamilton, Wolpert, & Frith, 2004; Marquez, Ceux, & Wenderoth, 2011; Poliakoff, Galpin, Dick, & Tipper, 2010; Shim, Carlton, & Kim, 2004). However, although a number of these studies applied transcranial magnetic stimulation (TMS) (Alaerts et al., 2010; Marquez et al., 2011; Senot et al., 2011), no study has yet addressed the brain activity that is evoked by the task of judging weight from visually perceived stimuli. The visual observation of actions activates regions in the premotor and inferior parietal cortex (Rizzolatti & Craighero, 2004). The measurement of brain activity from imaging studies to biological motion is well established in a large number of studies, which have typically found blood oxygen level dependent (BOLD) activity in occipital, temporal, and intraparietal regions (Grossman et al., 2000). BOLD activity in premotor and somatosensory regions has been found as well for point-light biological motion stimuli (Saygin, Wilson, Hagler, Bates, & Sereno, 2004).

Motion and its perception are strongly affected in individuals suffering from chronic pain (de Lussanet et al., 2012, 2013). Chronic pain patients strongly change the way they move and coordinate (Hodges & Tucker, 2011). Also, patients with chronic pain often suffer from kinesiophobia and depression (Vlaeyen, Kole-Snijders, Boeren, & van Eek, 1995). Despite these changes in chronic pain patients, it is known that changes in the brain are detectable. Structures typically involved are the anterior cingulate cortex (ACC), the insula, somatosensory regions (primary and secondary somatosensory cortex SI and SII), and the cerebellum (Apkarian, Bushnell, Treede, & Zubieta, 2005; Price, 2000). Thus, chronic pain is associated with problems of the sensorimotor system as well as with altered processes and structures in the brain.

It is well accepted that chronic pain may interfere with high-level cognitive processes (Kunz, Prkachin, & Lautenbacher, 2009; Rainville et al., 2011; Seminowicz & Davis, 2007). For example, pain-related words are processed differently in different populations of chronic pain patients (Eck, Richter, Straube, Miltner, & Weiss, 2011; Weiss, Miltner, & Dillmann, 2003). Also, patients with chronic back pain are specifically impaired when judging the manipulated weight from visually presented actions (de Lussanet et al., 2013). Due to this impairment chronic pain patients cannot judge the differences in the manipulated weight if the movement involves the body part that is affected in the patient (de Lussanet et al., 2012, 2013). In the latter study, two kinds of movements were presented with a range of different weights: manual transfer where a weight was transferred from the right to the left side using the upper extremities (Fig. 1B) and a trunk rotation where a weight is lifted and transferred from the right to the left side using the whole body (Fig. 1A). Subjects with shoulder pain were specifically impaired in weight assessment for manual transfer while subjects with low back pain were specifically impaired in weight assessment for trunk rotation.

How can this result be explained? We hypothesized that chronic pain interferes with the cortical regions that are usually recruited when viewing point-light biological motion with the instruction to judge the manipulated weights. We expected that the weight judgment task in healthy subjects should recruit the brain regions that are known to be affected in chronic pain patients. Thus, the goal of the present study was to measure the BOLD activity of healthy subjects in a functional MRI (fMRI) experiment during the presentation of point-light biological motion where different weights were lifted with the task to rate these weights.

We aimed to characterize the structures that are activated during the weight lifting tasks. We were also interested in the difference of activation between the two different kinds of movement, i.e., manual transfer versus trunk rotation. Finally, we wanted to compare those structures activated during the

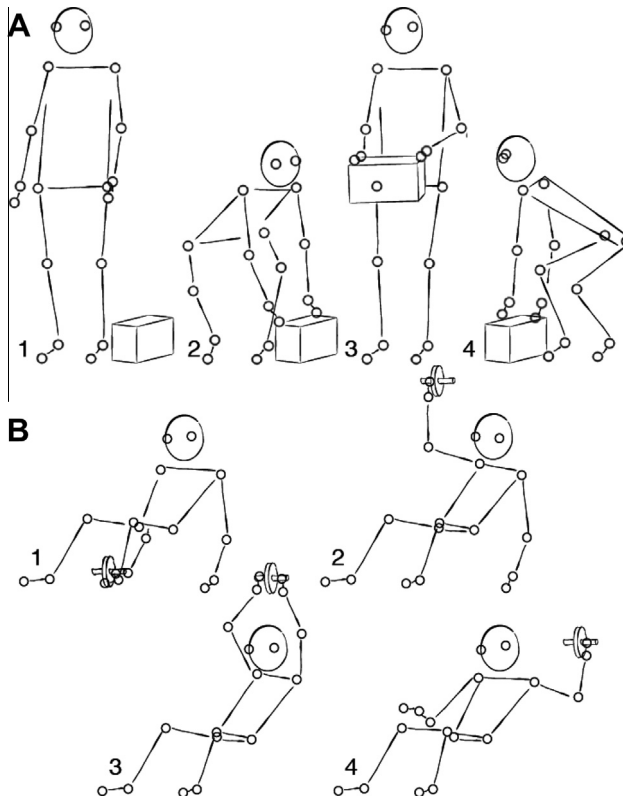


Fig. 1. Static representations of two of the point-light stimuli. (A) Trunk rotation. (B) Manual transfer. In the experiments only the points were visible; the connecting lines are for illustrative purpose only.

assessment of lifted weights with structures belonging to the neuromatrix of pain (Apkarian et al., 2005).

2. Methods

2.1. Subjects

Fifteen healthy, right-handed (Oldfield, 1971) subjects (2 male, 13 female, 19–31 years) volunteered in the fMRI experiment. Subjects were informed about the procedure of the experiment and provided written informed consent. The experiment used movies with either a trunk rotation or a manual transfer movement of weights in two classes to investigate the activation of the brain by means of fMRI. No subject had a history of neurological, psychiatric or pain disorder. Subjects were paid €6 for participating in the experiment. They were free to withdraw from the experiment at any time. The procedure was approved by the local ethics committee of the Friedrich Schiller University.

2.2. Visual stimuli

Computer-animated point-light stimuli (Fig. 1) were computed from recorded kinematic data from two healthy actors (one male and one female; Qualisys Motion Capture Systems) and depicted trunk rotation and manual transfer movements, displayed as white dots moving against a dark background

(Fig. 1). On the day before the recordings each actor practiced the timing of the movement sequences without load, against a metronome. For the recordings, the same movement was performed several times, each time with a different weight, again against the metronome. The actors never knew which weight they were to move. Thus it was secured that the movements of different weights followed exactly the same sequence and had the same timing (de Lussanet et al., 2012). A scrambled version of each scene presented the same dots each with a random offset such that the bounding box of the scene was conserved. The figures depicted in the movies carried different weights determining the four conditions of this experiment: manual transfer movements were presented with 3.5 and 7.5 kg, and trunk rotation movements were presented with 7.5 and 15 kg. The loads in the trunk rotation movements were twice as high as those of the manual transfer movements, so that the load on each hand was the same in each of the movement kinds. The low weights were perceived as “easy” and the heavy ones as “quite difficult” to manipulate by the actor.

2.3. Experimental procedure

The stimuli were projected (Presentation 16.3) via a video beamer onto a screen mounted to the head coil of the scanner. To familiarize the participants with the experimental hardware, each subject received a brief demonstration of the adjusting wheel for the weight rating prior to the experiment. Participants were naive about the purpose of the experiment. The subjects were instructed to focus on the movement of the figures displayed and to estimate the weight of the item moved using the adjusting wheel. The adjusting wheel moved a pointer underneath a scale ranging from 0 to 25 kg in steps of 1 kg. One example of a movie and a subsequent weight rating were presented in order to familiarize the participants with the experimental procedure. Each participant completed one experimental run of 14 minutes duration. The experimental design is displayed in Fig. 2. Each condition, followed by the weight rating, was presented 5 times throughout the experiment. On each trial, the movie sequence was shown twice. The order of the 20 trials (4 different conditions) was pseudo-randomized with the restriction that the same condition was not presented twice in succession. On each trial, the experimental condition was preceded by one movie with scrambled point-light stimuli followed by a 1-s fixation cross.

2.4. Image acquisition

Scanning was performed with a 3T magnetic resonance scanner (Tim Trio, Siemens Medical Systems, Erlangen, Germany). The experiment started with a high-resolution T1-weighted scan of the brain (192 slices, TE = 5 ms, FOV: 256×256 mm, resolution: $1 \times 1 \times 1$ mm) for anatomical referencing and visualization. A shimming procedure preceded the succeeding functional MR scanning. The first two volumes were discarded in order to improve field homogeneity. In the experimental fMRI run, 250 volumes were acquired using a T2* weighted echo-planar sequence (TE = 61 ms, TR = 3.7 s; FOV = 192×192 mm). Each volume comprised 60 slices (2 mm thickness and 2×2 mm in-plane resolution) which were prescribed parallel to the AC–PC plane).

2.5. Analysis of behavioral data

Performance data were analyzed with SPSS 13.0 (SPSS Inc., Chicago, IL). The average weight rating scores of each subject for each movement condition were submitted as dependent variable to an

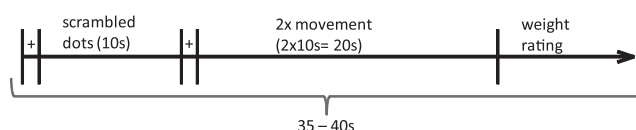


Fig. 2. Time course of one trial of the fMRI paradigm. The fixation cross (+) was presented for 0.6 s. The fixation crosses and the rating mask were preceded by a blank screen of 1.5 s, 0.5 s and 2.0 s respectively.

analysis of variance (ANOVA) with repeated measures on WEIGHT (high versus low) and MOVEMENT (trunk rotation versus manual transfer) as within-subject factors to detect differences regarding the subjective weight estimations between the particular conditions.

2.6. fMRI Preprocessing

Preprocessing and analysis of fMRI data was performed using BrainVoyagerQX 2.1 (Brain Innovation, Maastricht, The Netherlands). Primarily, all volumes were realigned to the first volume in order to minimize effects of head movements on data analysis. Further data preprocessing comprised spatial (6 mm full-width half-maximum isotropic Gaussian kernel) and temporal smoothing (high pass filter: 4 cycles per run; low pass filter: 2.8 s; linear trend removal) (Richter, Eck, Straube, Miltner, & Weiss, 2010; Straube, Schmidt, Weiss, Mentzel, & Miltner, 2009; Weiss et al., 2008). The anatomical and functional images were co-registered and normalized to the Talairach space (Talairach, 1988).

2.7. fMRI Statistical Analysis

Statistical analyses were performed by multiple linear regression of the signal time course at each voxel. The expected BOLD signal change for each condition (predictor) was modeled by a canonical hemodynamic response function. A random-effects General Linear Model was used to identify associated brain activity in all acquired slices. To minimize false-positive results, we tested whether the detected clusters survived a correction for multiple comparisons (Goebel, Esposito, & Formisano, 2006). Similarly to previous experiments (Richter et al., 2010; Straube et al., 2009; Weiss et al., 2008), we used the approach as implemented in BrainVoyagerQX2.4, which is based on a 3D extension of the randomization procedure described by Forman et al. (Forman et al., 1995). This procedure is based on the estimate of the map's spatial smoothness and on an iterative procedure (Monte Carlo simulation) for estimating cluster-level false-positive rates. After 1000 iterations, the minimum cluster size threshold that yielded a cluster-level false-positive rate of 5% was applied to the statistical maps. Clusters reported here survived this control of multiple comparisons. The location of significantly activated clusters was assessed by superimposing the results from group analysis on an averaged brain using NeuroElf v0.9c.

To estimate the overall BOLD response for the task, the biological motion sequences were contrasted against the scrambled sequences. We also contrasted the BOLD responses for the trunk rotation and the manual transfer movements to evaluate the differences in somatotopic activation. In order to estimate the influence of the weight of the transferred object we conducted a conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005) between the contrasts manual transfer 7 kg versus manual transfer 3.5 kg and trunk rotation 15 kg versus trunk rotation 7 kg.

3. Results

3.1. Performance data

The behavioral performance of all participants was poor. Eight subjects rated the higher weight higher than the lower weight on average over the 10 realizations for the trunk rotation movement and just 4 subjects over the 10 realizations for the manual transfer movement. Only two subjects rated the higher weight (marginally) higher than the lower weight in both movement conditions. Thus, the differences in the judgments of light versus heavy weights were close to guessing probability (Fig. 3). Consequently, we did neither find significant main effects for factors the weight ($F(1, 15) = 0.696$) and movement ($F(1, 15) = 0.243$) nor a significant interaction between factors the weight and movement ($F(1, 15) = 0.115$).

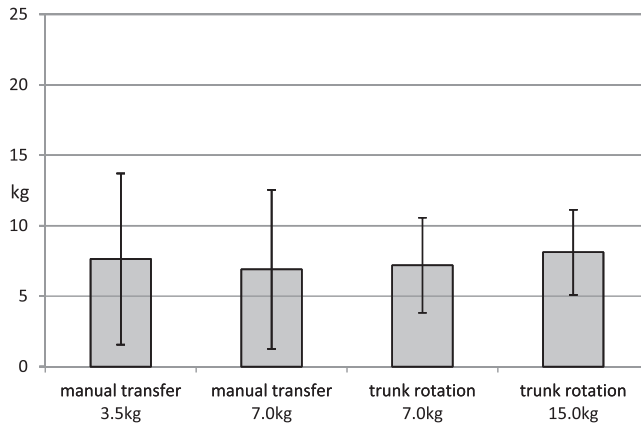


Fig. 3. Subjective weight ratings (mean and SD, in kg, $N = 16$) to manual transfer and trunk rotation movements.

3.2. Neuroimaging data

When comparing the activation while participants were watching point-light movements (manual transfer and trunk rotation) with the activation while scrambled light point stimuli were shown, we found significantly higher activation in a number of structures (Fig. 4, Table 1) including the primary visual cortex (V1), the fusiform gyrus bilaterally, the right superior temporal gyrus (STG), the primary sensory cortex (SI), the primary motor cortex (MI), the premotor cortex, the medial prefrontal cortex (mPFC), the left insula (INS), and the anterior cingulate cortex (ACC). There were cerebellar clusters in the right culmen and the left declive.

The scrambled movements evoked significantly higher BOLD activity in the left lentiform nucleus, the anterior end of the left STG, the middle frontal gyrus, the inferior parietal lobule (IPL), and the posterior cingulate (PCC).

Comparing the two kinds of movement, we observed extensive activations (Fig. 5, Table 2). For manual transfer versus trunk rotation these included activations in the precuneus, the middle and inferior temporal gyrus extending to the fusiform gyrus. There were parietal and dorsolateral prefrontal regions, as well as the hand and arm region of the MI (Talairach coordinates $-43, 0, 24$) and SI (Talairach coordinates $-5, -51, 68$; see Table 2).

For trunk rotation the activation was higher in the V1, the cuneus, the right middle temporal gyrus, the perigenual ACC, and the left anterior insula. Here too, there was an increased activity in SI (Talairach coordinates $-7, -37, 70$), although this did not survive the statistical correction. This activation was located in the back-region of somatosensory homunculus.

Consistent with the poor performance in the weight rating task, the conjunction of the contrasts manual transfer 7 kg versus manual transfer 3.5 kg and trunk rotation 15 kg versus trunk rotation 7 kg did not reveal any significantly activated clusters throughout the whole brain at an uncorrected cluster threshold of $p > .01$.

Finally, we analyzed the signal change in the ACC over the time course of our experimental blocks to investigate whether the activity is related to biological motion. In all conditions, the BOLD activity reached its maximum during the second presentation of the action sequence (Fig. 6). Activity returned almost to baseline by the beginning of the response period (Fig. 6).

4. Discussion

When judging the weight that is manipulated in visually displayed point-light stimuli, healthy participants show BOLD activity in the anterior cingulate, the insula, as well as in the somatosensory cortex and the cerebellum. The contrast of activation between manual transfer and trunk rotation

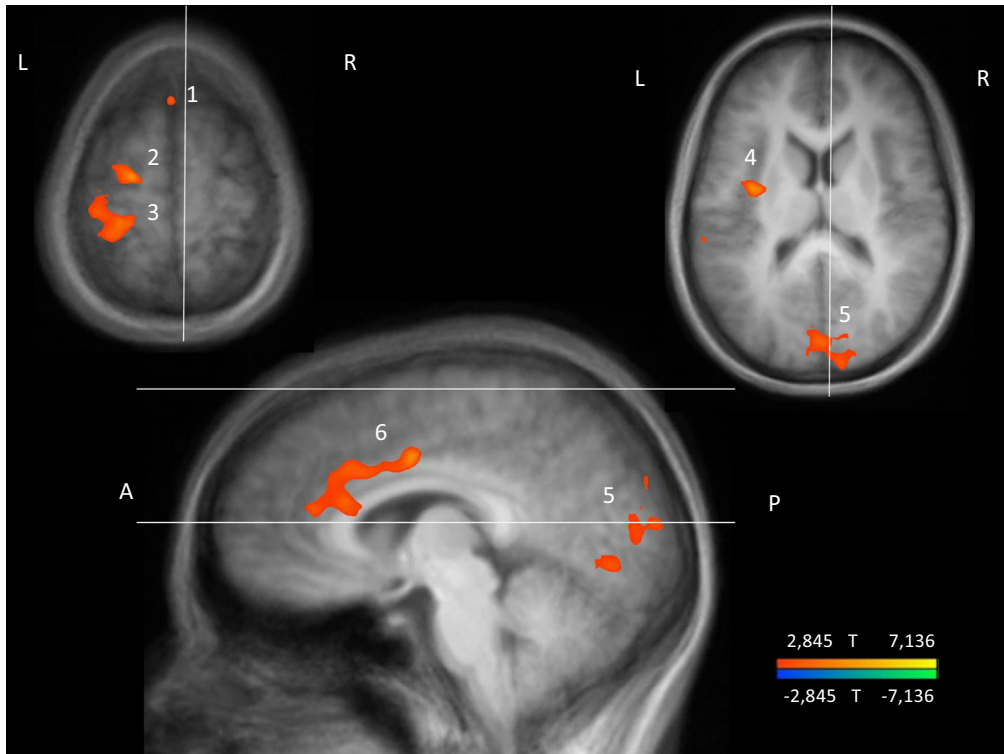


Fig. 4. Comparison of activations between movement and scrambled dots. The figure indicates that there are activations for movement (manual transfer and trunk rotation) vs. scrambled dots. Significant activations are rendered onto slices of an averaged T1 weighted brain image of all participants. The statistical threshold was $p > .05$ (cluster-corrected, 23 adjacent voxels). 1, medial prefrontal cortex; 2, premotor cortex; 3, SI/MI; 4, insula; 5, cuneus; 6, ACC; Talairach coordinates: left: $Z = 64$, middle: $X = 7$, right: $Z = 16$.

movement shows a clear somatotopy in the somatosensory region. Unexpectedly, none of the subjects was able to report differently to the different weights. Neither did we find weight-related differences in the BOLD activity.

4.1. Behavioral data

The lack of a behavioral effect was unexpected but consistent across subjects. Only two of the subjects rated the heavier weights of both movement kinds as heavier than the lower weights, and even in these two subjects, the indicated differences were very small (less than the 1-kg steps on the response mask). The behavioral results were consistent with the conjunction analysis, which revealed no weight-related activities even at a non-corrected significance level.

The stimulus material was selected from a previous study where the healthy controls were well able to recognize the differences between the presented weights (de Lussanet et al., 2012), and similar to the stimuli used in other studies (de Lussanet et al., 2013; Runeson & Frykholm, 1981). We also tested the stimulus protocol of this experiment outside the scanner, and confirmed that subjects were able to recognize the weights. In one more control we found that subjects could discriminate between the weights when they were lying supine outside the scanner, and when they were explicitly instructed to remain still while body movements were recorded.

For the further discussion of our results it seems important to consider the lack of correct weight assessment. According to their verbal reports outside the scanner, the subjects did try to assess

Table 1

Increases in activation for movement compared to scrambled movement. For composite clusters, the local maxima (LM) are listed additionally.

X	Y	Z	Size of cluster	side	t value	Anatomical localization	BA
–8	–81	1	470	L	6.661	Lingual Gyrus	
						LM, Cuneus (–4, –77, –3; $t = 5.83$)	18
28	–40	–26	156	R	5.824	Culmen	
–38	–6	15	56	L	5.470	Insula	
3	18	33	351	R/L	5.287	Cingulate Gyrus	24
–1	21	51	24	R/L	5.151	Superior Frontal Gyrus	6
–19	–11	63	40	L	4.733	Middle Frontal Gyrus	6
–37	–77	–26	38	L	4.229	Declive	
–24	–32	65	62	L	3.917	Postcentral Gyrus	3
					3.895	LM, Postcentral Gyrus (–25, –38, 65; $t = 3.896$)	5
					3.829	LM, Precentral Gyrus (–35, –29, 64; $t = 3.829$)	4
49	5	–2	25	R	3.918	Superior temporal Gyrus	22
–38	–49	40	225	L	–3.877	Inferior Parietal Lobule	40
–34	10	–26	501	L	–4.276	Superior temporal Gyrus	38
–7	2	–6	714	L	–4.583	Sub-lobar, Extra-Nuclear, White Matter	
						LM, Lentiform Nucleus (–6, 3, –4; $t = 3.981$)	
–36	33	–12	237	L	–4.842	Middle Frontal Gyrus	11
44	–36	–6	759	R	–4.869	Temporal Lobe, Sub-Gyral, White Matter	
–14	–44	20	392	L	–4.930	Sub-lobar, Extra-Nuclear, White Matter	
						LM, Posterior Cingulate (–13, –50, –19; $t = –3.375$)	

All reported peaks passed a whole-brain cluster-threshold level of $p > .05$, and were required to be at least 23 connected voxels in volume. Coordinates refer to the Talairach space (Talairach & Tournoux, 1988). BA, Brodmann area; R, right hemisphere; L, left hemisphere; LM, local maximum.

properly. We therefore believe that the fMRI activations we found are necessary to be engaged in the weight lifting task, while they are not sufficient to perform this task correctly. Thus, we assume that the brain regions we found activated during the processing of biological motion stimuli are representative for the conduction of the weight rating task.

The lack of a behavioral effect was unexpected as healthy participants are usually able to perform cognitive tasks in the scanner. Moreover, in pilot experiments we found that subjects were able to judge the weights well, even when lying still in a supine position. A possible, though unspecific, explanation for the lack of weight recognition might be a generally higher arousal due to the conditions inside of the scanner. Another factor that might have made the judgments more difficult than in other studies (e.g., Runeson & Frykholm, 1981) is that the recording of the actions was timed with a metronome to ensure that the durations were the same. Although the same recordings have been used earlier, it might be that the combination of the arousal in the scanner and the relatively exact timing of the movements caused the lack of behavioral effects.

4.2. BOLD activity during weight lifting task versus scrambled dots

Assessment of biological motion stimuli was accompanied by extended activations in occipital, ventral temporal and middle temporal regions. These activations are expected and in line with the literature (Grèzes, Costes, & Decety, 1998; Grèzes et al., 2001; Lestou, Pollick, & Kourtzi, 2008; Michels, Kleiser, de Lussanet, Seitz, & Lappe, 2009; Muthukumaraswamy, Johnson, Gaetz, & Cheyne, 2006; Pelphey, Morris, Michelich, Allison, & McCarthy, 2005; Ptito, Faubert, Gjedde, & Kupers, 2003; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). These regions are usually considered as belonging to the typical visual processing routes in the brain.

Central to our research questions are pain-related brain regions that interfere with activations during the weight lifting task. Activated brain regions for biological motion were found in the frontal lobe and the postcentral part of the parietal lobe. The strictly somatotopic organization of the primary somatosensory cortex serves – among others – the discrimination of the potentially tissue-damaging sensory stimulation (Bushnell et al., 1999). Even when painful events are observed in others, S1

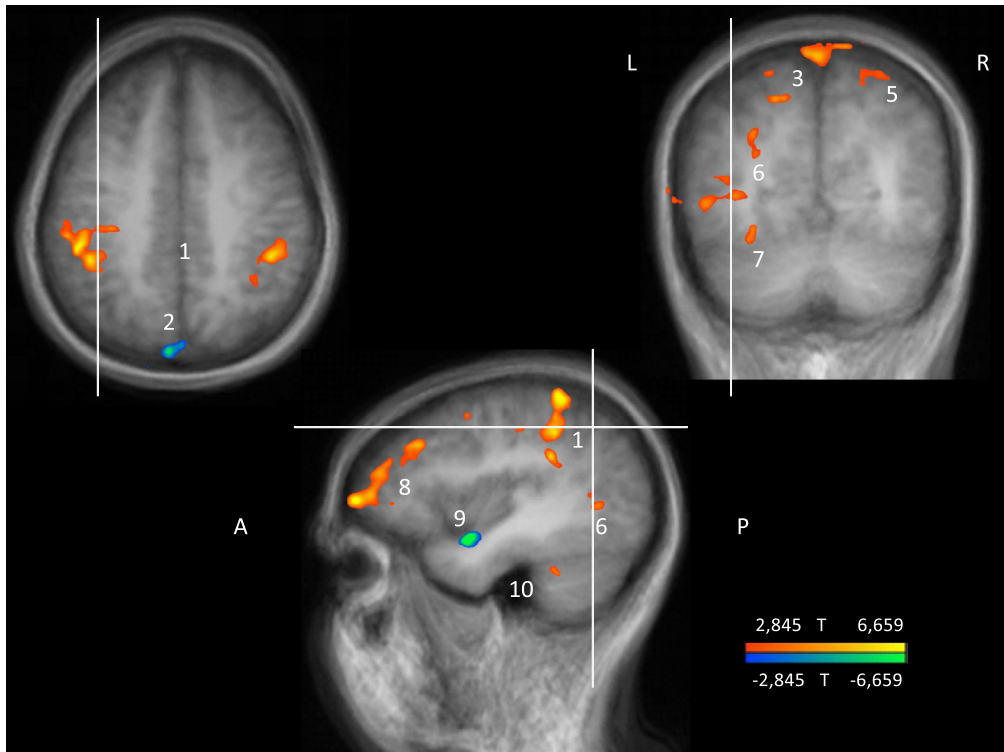


Fig. 5. Regions of significantly increased and decreased activations for manual transfer compared to trunk rotation movements. Significant activations are rendered onto slices of an averaged T1 weighted brain image of all participants. The statistical threshold was $p > .05$ (cluster-corrected, 27 adjacent voxels). 1, inferior parietal lobule (BA40), postcentral gyrus; 2, cuneus; 3, precuneus; 5, superior parietal lobule (BA7); 6, medial temporal gyrus; 7, fusiform gyrus; 8, medial frontal gyrus (BA6); 9, insula; 10, culmen; Talairach coordinates: left: $Z = 43$, middle: $X = -38$, right: $Y = -59$.

activity is modulated (Martinez-Jauand et al., 2012). Although the frontal lobe activity may not have a unitary role in pain processing, especially activity in prefrontal regions during painful stimulation is generally linked to attentional and cognitive processing of the painful event (Bornhove et al., 2002; Tolle et al., 1999). Modulation of prefrontal cortex activity was also found during expectations subjects made about painful events (Wager et al., 2004).

Another region we found activated and that is typically involved in the processing of pain-related stimuli is the ACC. It is thought that the ACC plays a role in representing the affective nature of pain and painful stimuli (Vogt, 2005). One may ask whether seeing someone lifting a heavy object might be responsible for the ACC activity in our study. The ACC (and the MCC) are often found activated by biological motion stimuli, even when any emotion, conflict, or pain is avoided. Similar activity of ACC has been found in many studies, whether displayed as point-lights (Dayan et al., 2007; Grèzes et al., 1998, 2001; Lestou et al., 2008; Pelphrey et al., 2005; Pito et al., 2003; Vaina et al., 2001), as stationary images (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006; Binkofski et al., 1999; Wheaton, Thompson, Syngienotis, Abbott, & Puce, 2004), or as movies (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Corradi-Dell'Acqua, Tomasino, & Fink, 2009; Lausberg & Cruz, 2004; Muthukumaraswamy et al., 2006; Salomon, Malach, & Lamy, 2009). Since only one of these studies showed transitive stimuli (Lestou et al., 2008) it seems highly unlikely that the ACC activity in our study is solely due to the presentation and judgment of the handled weight. This interpretation is supported by the time course of the BOLD signals (Fig. 6). For all four kinds of stimulus blocks, the BOLD response in the ACC region rose during the presentation of biological motion, reaching a maximum

Table 2

Increases and decreases in activation for manual transfer compared to trunk rotation movement. For composite clusters, the local maxima (LM) are listed additionally.

X	Y	Z	Size of cluster	side	t value	Anatomical localization	BA
–34	–73	19	58	L	7.643	Middle Occipital Gyrus	19
27	–71	50	197	R	6.623	Precuneus	7
–43	48	4	44	L	6.208	Middle Frontal Gyrus	46
–36	–47	22	679	L	6.069	Superior Temporal Gyrus	13
–29	–58	30	51	L	5.980	Middle Temporal Gyrus	39
53	31	16	121	R	5.800	Inferior Frontal Gyrus	46
				R		LM, Middle Frontal Gyrus (50,35,17; $t = 5.537$)	46
–5	–51	68	158	L	5.673	Postcentral Gyrus	7
30	–94	9	111	R	5.472	Middle Occipital Gyrus	18
19	–3	55	110	R	5.351	Medial Frontal Gyrus	6
–60	4	–4	48	L	5.271	Superior Temporal Gyrus	22
–60	–63	0	56	L	4.916	Inferior Temporal Gyrus	37
47	–34	47	90	R	4.838	Inferior Parietal Lobule	40
15	17	31	62	R	4.567	Anterior Cingulate	
–43	0	24	39	L	4.447	Precentral Gyrus	6
–21	–96	2	37	L	4.407	Middle Occipital Gyrus	18
–32	–58	–18	39	L	4.300	Declive	
–49	–70	7	235	L	4.254	Middle Temporal Gyrus	39
49	7	26	40	R	4.253	Inferior Frontal Gyrus	9
–18	–58	42	63	L	4.162	Precuneus	7
–20	–59	60	98	L	4.080	Precuneus	7
30	–57	34	44	R	4.003	Angular Gyrus	39
–30	1	48	40	L	3.939	Middle Frontal Gyrus	6
–3	–73	–11	30	L/R	3.798	Declive	
–11	–86	–4	64	L	–4.223	Lingual Gyrus	17
13	34	–1	71	R	–4.619	Medial Frontal Gyrus	10
				R		LM, Anterior Cingulate (11,37,–5; $t = 4.418$)	
–6	–82	37	98	L	–4.796	Cuneus	
–15	61	–1	27	L	–4.863	Superior Frontal Gyrus	10
2	–83	16	183	L/R	–4.868	Cuneus	
63	–27	–11	77	R	–5.199	Middle Temporal Gyrus	31
14	14	60	28	R	–5.736	Middle Frontal Gyrus	6
–40	0	–13	52	L	–6.246	Insula	

All reported peaks passed a whole-brain cluster-threshold level of $p > .05$, and were required to be at least 27 connected voxels in volume. Coordinates refer to the Talairach space (Talairach & Tournoux, 1988). BA, Brodmann area; R, right hemisphere; L, left hemisphere, LM, local maximum.

well before the end of the biological motion stimuli and returned to baseline by the beginning of the response period.

In fact, the above incomplete list of studies shows hardly any general correspondences, other than that the presented material contained human actions or implied actions. For example, the tasks were very different, and these stimuli sometimes showed the whole body but in many studies only one part of the body, such as a hand, mouth or foot. Since the grey matter volume of the OCC in macaque monkeys depends strongly on the size of their social network (Sallet et al., 2011), one might expect that the human ACC always becomes active when human activities are observed.

We also found an activation of the insula during the weight lifting task. BOLD activity in the insular cortex is reported frequently in studies on the perception and recognition of biological motion (Saygin et al., 2004). Thus, our finding is in line with the literature.

There was no higher BOLD activity for biological motion in the posterior STS. However, the STS is found activated only in little more than half of the studies of biological motion (Grèzes et al., 2001). Remarkably, studies in which the subjects had a task that was specifically related to the biological motion STS showed less activity than scrambled motion (Peuskens, Vanrie, Verfaillie, & Orban, 2005; Porat, Pertzov, & Zohary, 2011; Yamamoto, Someya, Troje, Ogawa, & Watanabe, 2009).

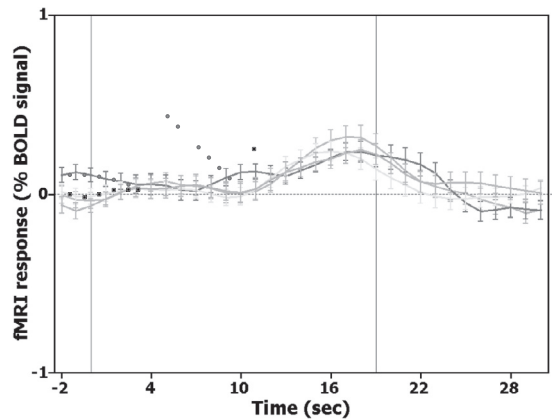


Fig. 6. Time course of the BOLD responses in the ACC during the presentation of the biological motion stimuli (trunk rotation 7.0kg, manual transfer 7.0kg, manual transfer 3.5kg, trunk rotation 15kg) and the response period. Time = 0: beginning of the first movie. Vertical line: end of the biological motion stimulus. The response period was variable (RANGE).

Overall, we found a generally higher activation for biological motion sequences as compared to scrambled motion. This higher activation is also not surprising. One reason for the higher activation might be the higher saliency of biological stimuli over unstructured stimuli. Biological motion stimuli can be expected to have received higher saliency due to their task-relevance (Taylor, Seminowicz, & Davis, 2009).

4.3. BOLD activity for manual transfer versus trunk rotation

Comparing the BOLD activity between both movement conditions, we found a clear somatotopy in the somatosensory regions. A somatotopy has been found in an fMRI study of mouth, hand, and foot actions, respectively, with static images as stimuli (Buccino et al., 2001).

In the present study, the manual transfer evoked a pronounced increase of BOLD activity in the hand and arm area of SI. The weight of the dumbbell in the manual transfer movements was half of that of the box in the trunk rotation movements. Therefore the load on each hand of the displayed actors was the same on average for the manual transfer and the trunk rotation movements. However, the stabilizing of the dumbbell and the transfer to the other hand requires much more manual control than the manipulation of a box hold in both hands (as in the manual transfer movement). Thus, it was expected that the manual transfer movements should evoke a higher BOLD activity in the hand and arm region of SI than the trunk rotation movement.

Conversely, the trunk rotation evoked a higher BOLD response in the trunk and back region of SI, although this activity did not survive the correction for multiple comparisons. The latter activity was expected, because the trunk rotation involves loading, movement, and fine coordination of the low back. In the manual transfer movement, on the other hand, the back remained motionless and unloaded.

The higher activations for the manual transfer movement as compared to the trunk rotation movement in frontal and mediotemporal areas were not expected. The duration of the sequences was the same, but the average velocity of the dots was about three times higher for the manual transfer movements than for the trunk rotation movements, even if the overall amount of movements of the dots is nearly identical. The higher average velocity of the point-lights might explain the increased BOLD activity in motion selective areas such as the mediotemporal gyrus.

4.4. Weight lifting task with respect to results in chronic low back pain

Our results, especially the activations in the primary and secondary somatosensory cortex (S1, S2), the anterior cingulate cortex (ACC), and the insula (INS), are of considerable interest with respect to

previous findings in chronic pain patients while viewing similar point-light motion stimuli (de Lussanet et al., 2013). It has been shown that chronic pain in a body part interferes with the ability to discriminate the manipulated weight when the manipulation involves movements of the painful body part, but not for other movements not involving that body part (de Lussanet et al., 2012). Additionally, the amount of handling usually helps healthy subjects to better judge the weight, while this is not the case in pain patients. In contrast, more handling interferes more strongly in chronic pain patients (de Lussanet et al., 2013). The results presented here offer a possible explanation for the impairment of weight judgment in pain patients. On the one hand, we demonstrated that the judgment of manipulated weights from point-light biological motion is associated with the activation of S1, S2, ACC, and INS. On the other hand, there are numerous studies demonstrating the involvement of the same structures during the processing of noxious stimuli and pain (e.g., (Apkarian et al., 2005; Peyron, Laurent, & Garcia-Larrea, 2000; Weiss et al., 2008)). S1 and SII are thought to be involved in the processing of the somatosensory component of pain, while ACC and INS have been associated with the analysis of the emotional component of pain (Rainville, Roy, Piche, Chen, & Peretz, 2009; Tracey & Mantyh, 2007; Treede, Kenshalo, Gracely, & Jones, 1999) as well as saliency (Legrain, Iannetti, Plaghki, & Mouraux, 2011; Liang, Mouraux, & Iannetti, 2013). So it might be possible that the impaired judgment of manipulated weights in point-light motion stimuli in chronic pain patients results from an interference between of processing to judge weights and the processing of pain in one or several of these regions, i.e., S1, SII, ACC, and/or INS. More precisely, given that the impairment was found only for point-light biological motion that involves the affected body part, but not for movements of other body parts, it is more likely that the interference occurs at the level of S1 or SII, even when we cannot exclude ACC and INS definitely due to the homuncular organization of parts of these structures (Baumgartner, Vogel, Ohara, Treede, & Lenz, 2011).

4.5. Limitations and future directions

An unfortunate result of the present study was the finding that none of the subjects was able to perceive the differences in the manipulated weight, and correspondingly, the lack of weight-related differences in the BOLD responses. For this reason it is advisable to choose a different task for fMRI experiments. Moreover, this study would have benefited by another baseline condition in which point light-actors are shown that do not lift any weight. This would assure the specificity to the contrasted action more precisely than the scrambled conditions used in the present work.

Still, given that the different stimuli activated somatosensory regions in a somatotopic manner provides future possibilities for studying the changes in motor representations due to chronic pain in corresponding patient groups.

5. Conclusion

In summary, the investigation of point-light biological motion for two types of movements performed with different weights demonstrated strong activation of primary and secondary somatosensory regions, the anterior cingulate cortex, and the insula in healthy subjects. Probably, the activation of the somatosensory regions serves the judgment of weight information from the biological motion stimuli, while the activation of the anterior cingulate and the insula probably serves the integration of behaviorally relevant information. These findings provide important information for the understanding of mechanisms underlying the judgment task, but possibly also why chronic pain patients are impaired in this task. Finally, the somatotopic organization in the contrast of the two activities confirms earlier findings that different sensorimotor networks are recruited depending in the exact action that is visually presented.

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