MASTER

Do the neurons for intransitive actions show cross modal repetition suppression? an fMRI study

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Do the neurons for intransitive actions show cross modal repetition suppression? An fMRI study.

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Abstract

Mirror neurons have been found in Macaque monkeys, but in humans the evidence for existence of a Mirror Neuron System is not clear. For transitive actions (actions where objects are involved) good indications of Mirror Neuron System involvement has been shown (Chong et al., 2008; Kilner et al., 2009), but for intransitive actions the evidence is not found with repetition suppression (Dinstein et a., 2007; Lingnau et al., 2009). However, activation of Mirror Neuron System areas is found with conjunction analysis, but this is not strong proof of the involvement of the Mirror Neuron System.

With the use of fMRI we try to find evidence for the involvement of the Mirror Neuron System in humans for intransitive actions by looking for cross modal repetition suppression. Suppression should be found for repeatedly activated neurons, so if there are mirror neurons in humans, these neurons should be less highly activated for observation after execution of the same action.

Two mechanisms might underlie the lack of findings in the past: verbalization might be the cause of previously found repetition suppression effects and the reason why actions that cannot be verbalized do not show activation in the Mirror Neuron System. Or maybe meaningfulness is the underlying factor for the inconsistent findings for intransitive actions and lack of findings is due to the actions not having a predictable nature in previous studies.

The results were not significant, but an exploratory search showed interesting results that seem to indicate that all intransitive actions cause a response of the Mirror Neuron System and that there might not be underlying mechanisms. Instead, we speculate that the reason for a lack of findings with the repetition suppression paradigm for intransitive actions is that intransitive actions give a weaker response than transitive actions because less neurons are dedicated to intransitive actions than to transitive actions.

1. Introduction

The ability of humans to understand another person's action intentions is a remarkable ability in which the mirror neuron system (MNS; the MNS is comprised of bilateral ventral premotor/inferior frontal gyrus and rostral inferior parietal cortices) seems to play an important role (Chong, Cunnington, Williams, Kanwisher & Mattingley, 2008; Dinstein, Hasson, Rubin & Heeger, 2007; Gazzola & Keysers, 2009; Kilner, Neal, Weiskopf, Friston & Frith, 2009; Lingnau, Gesierich & Caramazza, 2009). Culminating evidence seems to suggest that the mirror neuron system connects observed actions to the individual' s own motor repertoire and thus cause the individual to understand another's intentions (Brass, Schmitt, Spengler & Gergely, 2007; de Lange, Spronk, Willems, Toni & Bekkering, 2008; Fogassi, Ferrari, Gesierich, Rozzi, Chersi & Rizzolatti, 2005; Newman-Norlund, van Schie, van Hoek, Cuijpers & Bekkering, 2010). However, the role of mirror neurons, originally found in macaque monkeys (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992), remains elusive. One cannot use the same invasive techniques in humans as in monkeys, and even the identification of homologous areas is problematic, because there are many functional differences. For example, mirror neurons in macaque monkey almost exclusively respond to observation and execution of transitive actions (monkeys don't use sign language or gestures), but the mirror neuron system in humans has been shown to respond to both transitive and intransitive actions (Dapretto, Davies, Pfeifer, Scott, Sigman, Bookheimer & Iacoboni, 2006; Fadiga, Fogassi, Pavesi & Rizzolatti, 1995; Fazio, Cantagallo, Craighero, D'Ausilio, Roy, Pozzo, Calzolari, Granieri & Fadiga, 2009; Iacoboni, Woods, Brass, Bekkering, Mazziotta & Rizzolati, 1999; Iacoboni, Koski, Brass, Bekkering, Woods, Dubeau, Maziotto & Rizzolatti, 2001; Jackson, Meltzoff & Decety, 2006; Koski, Iacoboni, Dubeaum Woods & Mazziotta 2003; Koski, Wohlschlager, Bekkering, Woods, & Dubeau, 2002; Maeda, Kleiner-Fisman & Pascual-Leone, 2002; Oosterhof, Wiggett, Diedrichsen Tipper & Downing, 2010; Patuzzo, Fiaschi & Manganotti, 2003; Pazzaglia, Smania, Corato & Aglioti, 2008), imagined actions (Bakker, de Lange, Helmich, Scheeringa, Bloem & Toni, 2008), imitation(Heiser, Iacoboni, Maeda, Marcus & Mazziotta, 2003; Iacoboni, 2009; Molenberghs, Cunnington & Mattingley, 2009; Tanaka & Inui, 2002), intention recognition(de Lange, Spronk, Willems, Toni, Bekkering, 2008; Fogassi Ferrari, Gesierich, Rozzi Chersi & Rizzolatti, 2005; Brass et al., 2007, Newman-Norlund et al., 2010), emotion (Dapretto et al., 2006), and the list keeps growing.

Mirror neuron research in humans has been mostly based on fMRI studies using conjunction analysis (Buccino, Binkofski, Fink, Fadiga, Fogassi, Gallese, … Freund, 2001; Calvo-Merino, Gaser, Grezes, Passingham & Haggard, 2005; Decety, Chaminade, Grezes & Meltzoff, 2002; Grafton, Arbib, Fadiga & Rizzolatti, 1996; Grezes, Costes & Decety, 1998; Grezes & Decety, 2001; Grezes, Armony, Rowe & Passingham, 2003; Iacoboni et al. 1999, Iacoboni et al. 2001; Koski et al. 2002, 2003; Manthey, Schubotz & von Cramon, 2003; Nishitani & Hari 2000, 2002; Perani, Fazio, Borghese, Tettamanti, Ferrari, Decety & Gilardi, 2001; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). With this method areas in the brain are located that are active both during execution and during observation. Needless to say, this method does not necessarily imply the existence of mirror neurons. Recently repetition suppression has become more popular as a method to investigate mirror neurons with fMRI (e.g. Dinstein, Hasson, Rubin & Heeger, 2007). This method locates areas in the brain based on reduced activity to repeated stimuli. It is commonly believed that neural adaptation underlies this phenomenon (Bartels, Logothetis & Moutoussis, 2008; Henson & Rugg, 2003; Larsson & Smith, 2011). Thus, this method can identify the neurons or neural populations that are active for both execution and observation.

In the context of mirror neurons we can invoke repetition suppression in four ways: repeated execution of an action, repeated action observation, action observation followed by action execution or the other way around. Not all possibilities are equally useful for locating mirror neuron areas. The first two sequences are typically used as controls as they do not include both action execution and action observation. The third sequence is often disputed because it could be simply showing a visual priming effect instead of a motor priming effect. So the remaining sequence, where action execution is followed by action observation is the stronger cross-modal sequence for location mirror neuron areas and is the sequence we will focus on.

Chong, Cunnington, Williams, Kanwisher and Mattingley (2008) showed the first cross modal repetition suppression effects in the Inferior Parietal Lobule for humans when the participants executed transitive meaningful movements in the scanner like “hammer nail” or “shoot gun”. Kilner, Neal, Weiskopf, Friston and Frith (2009) showed cross modal repetition suppression in the Inferior Frontal Gyrus in humans with transitive actions: People had to grasp a pin or pull a ring that were both attached to a box. Kilner et al. (2009) argue that the pin-grasping and ring-pulling are less meaningful actions than hammer-nailing and gun-shooting, because actions are more abstract and less commonly used (Kilner et al., 2009).

Unlike conjunction analysis, repetition suppression has not been fruitful yet in identifying the role of the Mirror Neuron System for recognizing intransitive actions. Dinstein et al. (2007) tested meaningful intransitive hand actions using the gestures from the Rock-Paper-Scissors-game but they did not find significant cross modal repetition suppression effects. Also Lingnua, Gesierich and Caramazza (2009) failed to find significant effects for intransitive meaningless hand gestures.

It is unclear why studies based on cross modal repetition suppression (Dinstein et al., 2007; Lingnau et al. 2009) fail to reproduce earlier results for intransitive actions (Dapretto et al., 2006; Fadiga et al., 1995; Fazio et al., 2009; Iacoboni et al., 1999; Iacoboni et al., 2001; Jackson et al., 2006; Koski et al., 2003; Koski et al., 2002; Maeda et al., 2002; Oosterhof et al., 2010; Patuzzo et al., 2003; Pazzaglia et al., 2008), but if intransitive actions show a cross modal repetition suppression effect then this shows that activation in the mirror neuron areas did not arise because of the association of an action with an object, but merely from observing and executing the action. This would make the claim that the mirror neuron system serves the purpose of action understanding more general (Lingnau et al. 2009).

A possible cause for not finding repetition suppression for intransitive actions could be the absence of meaningfulness in previous intransitivity studies. If actions are not meaningful it is not possible to predict what the action will look like because the goal or intention of the action is not clear and thus the predictability of an action is lost. Many studies have showed that intention is an important factor for the MNS to show activation (de Lange, Spronk, Willems, Toni & Bekkering, 2008; Fogassi, Ferrari, Gesierich, Rozzi, Chersi & Rizzolatti, 2005; Brass, Schmitt, Spengler & Gergely, 2007; Newman-Norlund, van Schie, van Hoek, Cuijpers & Bekkering, 2010; Umilta Kohler, Gallese, Fogassi, Fadiga, Keysers & Rizzolatti, 2001). So we will distinguish between meaningful and meaningless intransitive actions. The distinction between meaningful and meaningless is open to interpretation. We define a meaningful action as an action for which the goal or intention is clear. To make sure that the meaning of an action is clear to every participant we will therefore use actions that are familiar actions in Dutch culture. For meaningless actions we will take actions that Dutch people are not familiar with, so no goal or intention is attributed.

Also the MNS has an intricate relation with language. The language and motor system often get activated together (Aziz-Zadeh, Wilson, Rizzolatti & Iacoboni, 2006; Elk, van Schie & Bekkering, 2009; Gentilucci, Benuzzi, Gangitano & Grimaldi, 2001; Meister, Boroojerdi, Foltys, `sparing, Huber & Topper, 2003; Seyal, Mull, Bhullar, Ahmad & Gage, 1999; Tokimura, Tokimura, Oliviero, Asakura & Rothwell, 1996), but this interaction is restricted to the left hemisphere and only hand and mouth actions seem to be influencing each other (Aziz-Zadeh, Iacoboni, Zaidel, Wilson & Mazziotta, 2004; Rizzolatti & Craighero, 2004). When you speak, often you start to make gestures with your hands and it is difficult to repress hand actions while talking. Area F5 of the macaque brain is thought to be the homologue of the human brain area the Inferior frontal gyrus (IFG) (Rizzolatti & Craighero, 2004).. In area F5 mirror neurons are found that respond to hand or mouth actions (Ferrari, Gallese, Rizzolatti & Fogassi, 2003). The IFG contains Broca's language area, but is also active for movement preparation (thoenissen, Zilles and Toni, 2002), action recognition (Decety, Grezes, Costes, Perani, Jeannerod, Procyk, Grassi & Fazio, 1997, hamzei, Rijntjes, Dettmers, Glauche, Weiller & Buchel, 2003) and action execution and observation. Verbalization might be the cause of previously found repetition suppression effects (Chong et al., 2008; Kilner et al. 2009) and thus actions that cannot be verbalized might not show activation in the Mirror Neuron System. So we will compare actions that can be verbalized and actions that cannot be verbalized.

In this study we will focus on the role of mirror neurons in the processing of intransitive actions. Half of the intransitive actions are familiar and half are unfamiliar. Also we make a distinction between actions that are associated with a verbal label and secondly, actions which are not verbalized. This leads to a two by two design of familiarity against labeling, with four conditions: word-familiar, word-unfamiliar, symbol-familiar and symbol-unfamiliar. Of these four conditions the condition word-unfamiliar and symbol-familiar are most important to answer our research questions. Firstly, if we see CMRS for the words-unfamiliar and not in the symbol-unfamiliar condition, then the labeling appears to be essential for the mirror neuron system. Secondly, if we find CMRS for the symbol-familiar condition in contrast to the symbol-unfamiliar condition, then the meaningfulness of an action is proven to be a necessity for the mirror neuron system. Apart from the whole brain analysis we will also do a region of interest (ROI) analysis in bilateral IFG and IPL.

2. Materials & Method

Participants

15 right-handed healthy native Dutch speaking female students (21,7 years) participated in the experiment. Three participants moved more than 3 mm and were therefore excluded from analysis. All participants were unfamiliar with sign language and diving language. All gave written consent according to the institutional guidelines set forth by the local ethics committee (CMO region Arnhem-Nijmegen, the Netherlands) before the experiment. The participants were compensated 10 euro/hr or study credits for their participation.

Stimuli

The stimuli consisted of videos of hand actions and videos with labels for these actions (see appendix for stills of the videos). In total there were twelve actions. Six actions were categorized as familiar in the sense that the movements were commonly used actions for communication. The other six were unfamiliar, they are movements people execute often but have no common meaning attributed by people. Within both groups of actions another dissection was made in the type of label to instruct the participants with. Within each group of six actions three had labels in the form of words and three in the form of symbols. Eight of the twelve actions were straight from Lingnua et al.'s (2009) study to get a comparable experiment. The six symbols from this study are also from Lingnau et al. (2009). A brainstorm was held to find the remaining actions and word labels. The result was tested on a separate group of people. On eleven people the actions were tested for the frequency people came across them in daily life and what meaning they attributed to the actions. (See appendix for the questionnaire and statistics). Results showed that the categorization was good. It was also checked the other way around by showing ten different people the labels and asking them to make up a movement to go with it. This showed that an average of 8 out of 12 actions were guessed correctly. This shows that the labeling was intuitive. This was also shown in the preparatory practice session for the fMRI experiment where people did about ten actions correct after being shown the labels with the actions only once.

Procedure

The day before the scanning session participants were taught which labels belonged to which actions. This practice session took about fifteen minutes and ended when the participant could perform all actions without hesitation upon seeing the labels. The scanning session consisted of 5 blocks. The first four blocks were trials where participants were first shown a video with a label which cued them to execute a movement, followed by a video in which they saw the same action being performed by a female hand or by seeing a different action for the same condition. Only one type of condition was practiced per block, e.g. only the three actions with words as labels that were familiar. The order of the four blocks was counterbalanced across participants and the trials with the similar actions (30 trials) and the trials with different actions (30 trials) were shown in a randomized counterbalanced order within the blocks. The fifth block was appended to check if the experimental design was set-up correctly to show repetition suppression correctly. In this block the participants again viewed two movies. The movies showed only labels to indicate that they had to perform an action. Because the participant executed twice, we are sure that the same neurons are activated twice and thus we should see repetition suppression when the two actions were the same compared to actions following each other that were differed. We added this block to show that if we don't find CMRS cannot be accredited to a bad experimental design. Each block consisted of an instruction and 60 trials and lasted about 9 minutes. See figures 1 and 2 for a mock-up of the two types of trials. The hand actions made by the participants were recorded with a JVC Everio camcorder to check for mistakes after the experiment.

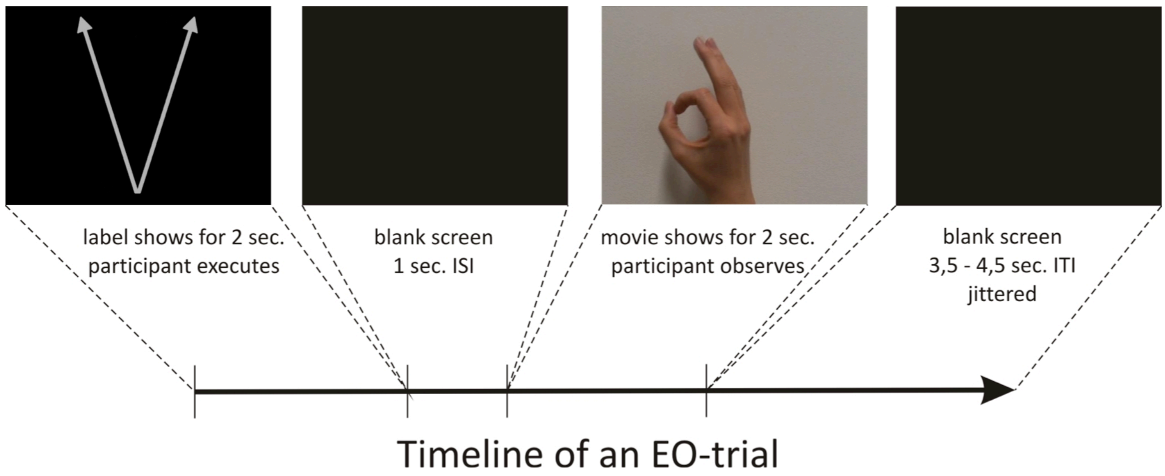

Figure 1: EO-trial, The images are stills of the movies that the participant viewed. In EO-trials the participant first watched a movie that depicts a label or word and at that time the participant would execute the associated action. After 1 second of blank screen the participant viewed a movie of a hand making the same or a different action. ISI = inter stimulus interval, ITI = inter trial interval.

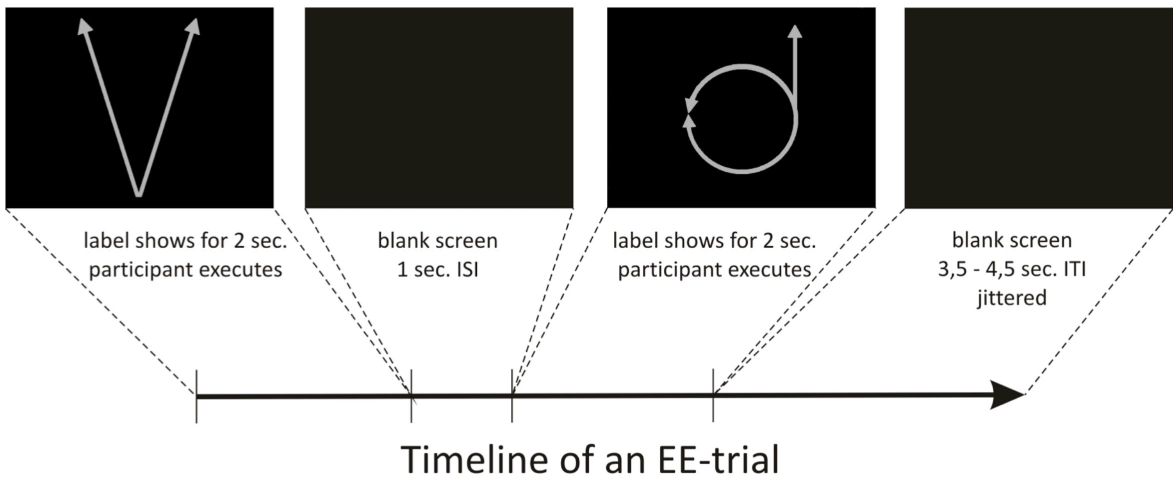

Figure 2: EE-trial timeline, in this case the articipant executed an action twice. The second action could be either the same or different. ISI = inter stimulus interval, ITI = inter trial interval.

fMRI data acquisition

Imaging was conducted at the F.C. Donders Centre for Cognitive Neuroimaging (Nijmegen, the Netherlands). The functional images were acquired on a Siemens Trio 3.0T MRI system with a multiecho sequence and a birdcage head coil (TR = 2.39 s, 5 TE's = 9.4 ms, 21.2 ms, 33 ms, 45 ms, 56 ms, 90 flip angle, 31 axial slices in ascending order, voxel size 3.5 x 3.5 x 3.5). Head movement was restricted by foam cushions and a strip of tape over the forehead. Blocks lasted about 10 minutes and at the end a high resolution anatomical images were acquired using an MPRAGE sequence (echo time = 3.03, voxel size = 1x1x1 mm, 192 sagittal slices, field of view=256).

fMRI data analysis

The images were preprocessed and analyzed with SPM8 (Statistical Parametric Mapping, http://www.fil.ion.ucl.ac.uk/spm). The first six dummy scans were removed. The functional images were corrected for small head movement by realigning them to the first image of the session. The five echoes were combined and then slice time correction followed. The images were co-registered to the anatomical image and then normalized to the Montreal Neurological Institute (MNI) template and smoothed using an isotropic 8mm FWHM Gaussian kernel.

The events of analysis for each condition were modeled as starting at the start of the associated videos and having no duration because the events lasted 2 seconds or less. The rest time was modeled by the instruction times and the faulty trials. A trial was declared faulty when participant executed the wrong movement and when they started the wrong movement but corrected themselves. Very little mistakes were made, zero to a maximum of eight on 360 trials, most of the errors occurred in the final block due to tiredness.

A statistical parametric map was estimated for every person for the same and different trials of all five blocks. For every person simple t-contrasts were made for the CMRS effect per condition using the General Linear Model. If CMRS occurred the BOLD response for two different actions should be higher that the BOLD response for twice the same action. So repetition suppression is calculated by subtracting the BOLD response of the same-trials from the BOLD response of the diff-trials for every condition. (Diff – Same = Repetition Suppression).

In the 2nd level analysis the participant's contrasts were grouped to form a new group level Statistical Parametric Map using the General Linear Model (significance threshold: uncorrected p = 0.001).

Table 1: overview of conditions and independent variables. On top the first four EO-blocks are visible, below the final EE-trial.

Execution - Observation Word -Familiar		Execution – Observation Word -unfamiliar		Execution - Observation Symbol - familiar		Execution - Observation Symbol -unfamiliar	
30 trials same action	30 trials different action	30 trials same action	30 trials different action	30 trials same action	30 trials different action	30 trials same action	30 trials different action

Execution - Execution Word -Familiar	
30 trials same action	30 trials different action

ROI analysis

Two bilateral ROIs were chosen based on CMRS findings in these locations in the literature: the inferior frontal gyrus (IFG) and the inferior parietal lobule (IPL) (Chong et al., 2008; Kilner et al., 2009). Based upon the MNI coordinates from the ANSIR laboratory WFU_Pickatlas (http://fmri.wfubmc.edu/software/PickAtlas, Maldjian, Laurienti, Kraft & Burdette, 2003) the voxels belonging to the IFG and IPL were selected. In figure 3 the location of the anatomical ROIs are visible as they appear in the WFU_Pickatlas (Maldjian et al., 2003). In these regions the peak CMRS coordinates were selected from the data form the execution-execution block and a spherical ROI of 10 mm was constructed around the four peak coordinates to use for the ROI analysis.

For the ROI analysis we did a full factorial by analyzing the CMRS effects in PASW18 using a Repeated Measures General Linear Model with a two by two design of labeling by familiarity to see if there are differences between action labeled by words or symbols, and to see if there are differences between actions that are familiar or unfamiliar.

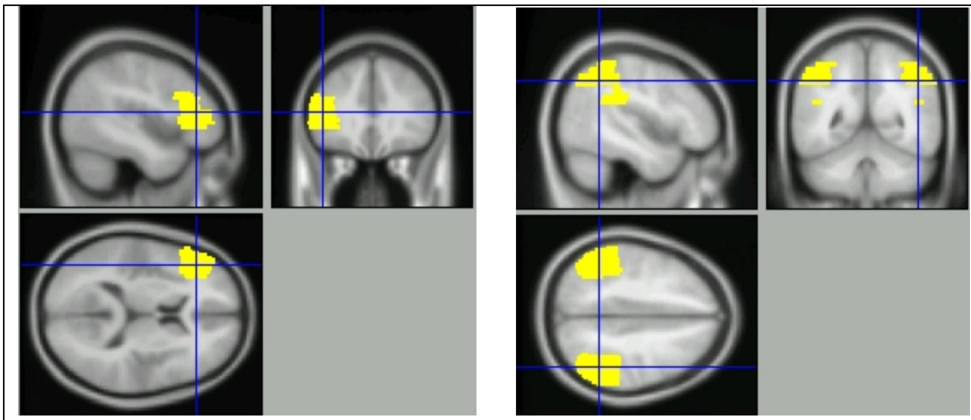

Figure 3: On the left the yellow blob shows the pars triangularis in the left inferior frontal gyrus. On the right the inferior parietal lobule for both sides is shown. Iamges are from the WFU_Pickatlas by ANSIR laboratory.

3. Results

Whole brain analysis

We did a whole brain analysis per block at an uncorrected $p < 0.001$ level.

Word-unfamiliar

The primary block to show an effect of labeling with words (word-unfamiliar) did not show CMRS effects in the IFG or IPL. The peak activations are sub gyral and all other active voxels are sub lobar or in the white matter of the occipital, frontal or parietal lobe.

Symbol-familiar

The primary block for familiar actions (symbol-familiar) showed very little CMRS effects. The highest peak was sub gyral and small activations were in the occipital lobe and in the middle frontal gyrus.

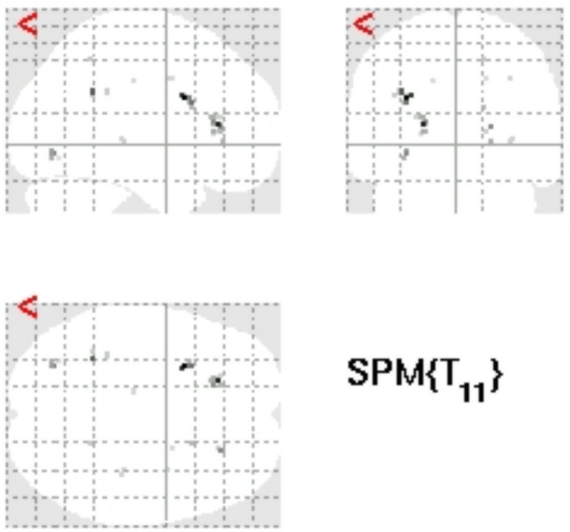

Figure 4: Glass brain showing the cross modal repetition suppression effect for word-unfamiliar at $p < 0.001$

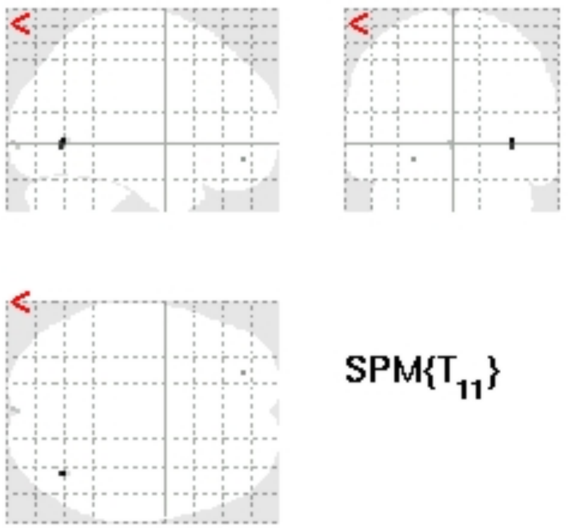

Figure 5: Glass brain showing the cross modal repetition suppression effect for symbol-familiar at $p < 0.001$

Word-familiar

For the block word-familiar we found the strongest CMRS at a sub lobar location. The other clusters are in the cingulated gyrus, corpus callosum, cerebellum and sub gyral in the frontal and parietal lobe.

Symbol-unfamiliar

For the block symbol-unfamiliar we expected to see no CMRS effects but we found a cluster of 23 voxels in the right IFG triangularis with peak MNI-coordinate [58 28 0]. All other CMRS activation is in the superior, middle and medial frontal gyrus.

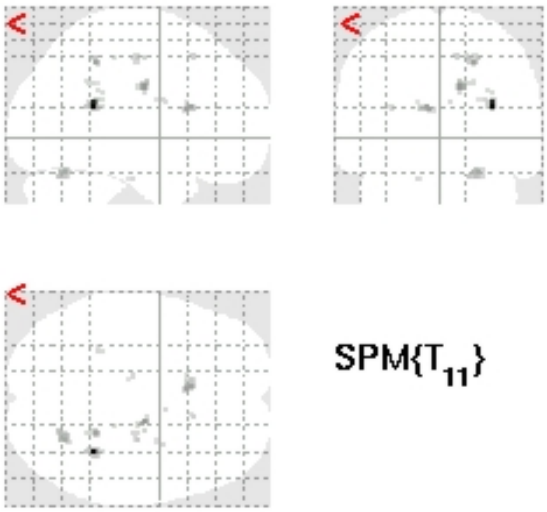

Figure 6: Glass brain showing the cross modal repetition suppression effect for word-familiar at $p < 0.001$

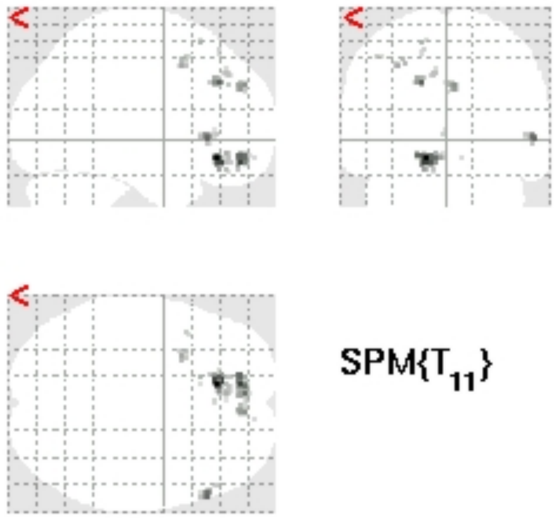

Figure 7: Glass brain showing the cross modal repetition suppression effect for symbol-unfamiliar at $p < 0.001$

Experiment control and localizer

The fifth block was added to use as a localizer for the ROI analysis Because the participants only executed actions, we are sure that the same neurons should be repeatedly activated in this block therefore this block is a control for the experimental set-up and should show repetition suppression effects.

At a $p < 0.001$ we see little activation. A cluster of 29 voxels with peak MNI value at [-36 20 16] of which 5 voxels are in the left IFG triangularis and 18 voxels in the IFG opercularis. Another two clusters are present but they are located in the temporal pole, which is not associated with the MNS.

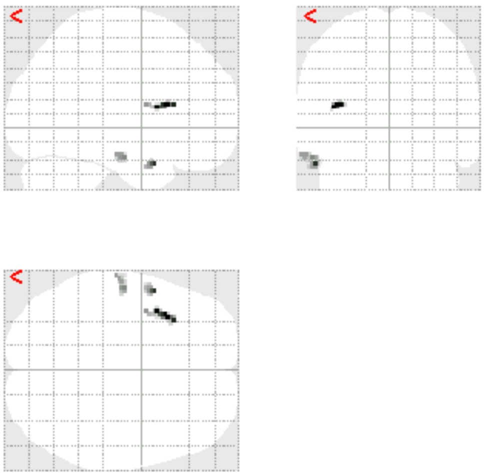

Figure 8: Glass brain showing the cross modal repetition suppression effect for the EE-block at $p < 0.001$

ROI analysis

There were no significant differences between the conditions, not at any ROI, as can be seen in table 2. In the right IPL for labeling the result came closest to significance with $p = .098$ but this effect was in the opposite direction of the hypothesis with symbol (mean = 0,045) having a higher mean CMRS effect than word (mean = -0,295). So no significant differences are found between word and symbol and between familiar and unfamiliar.

Table 2: Results of comparison between conditions, ROI analysis on bilateral IFG and IPL. F-statistics and P-levels are given in the first two columns and in the final four columns the mean and standard deviation can be seen by category.

	Condition Labeling	**Condition familiarity**	**Mean word (st. dev.)**	**Mean symbol (st. dev.)**	**Mean familiar (st. dev.)**	**Mean unfamiliar (st. dev.)**
Right IFG [42 36 2]	F = 1,536 p = .241	F = 1,402 p = .261	-0,008 (0,107)	0,209 (0,133)	-0,010 (0,115)	0,210 (0,133)
Left IFG [-36 20 16]	F = 0,196 p = .666	F = 0,477 p = .504	-0,036 (0,083)	0,021 (0,096)	-0,071 (0,074)	0,056 (0,139)
Right IPL [50 -64 42]	F = 3,279 p = .098	F = 1,057 p = .326	-0,295 (0,150)	0,045 (0,110)	-0,222 (0,133)	-0,028 (0,130)
Left IPL [-40 -40 32]	F = 1,998 p = .185	F = 2,503 p = .142	0,155 (0,058)	0,020 (0,075)	0,014 (0,051)	0,161 (0,079)

Exploratory results

We only see very little repetition suppression activation at $p < 0.001$ for the control block (EE). We expect a comparable level of significance for the other blocks. It might show that we should also not expect a lot of activation at $p < 0.001$ for all the other blocks. So to see if there is CMRS we might need to give our data a little more slack. As an exploration, we will take the significance level down to a level that makes more activation visible (about 1500 voxels) and then limit our search to bilateral IFG and IPL.

Word-unfamiliar

At a lower level of $p < 0.005$ we find a cluster with a peak value at MNI-coordinates [-34 -46 32] with 30 voxels in the left IPL. Also we found a cluster in the IFG at MNI coordinates [-48 8 28] with 14 left IFG voxels.

Symbol-familiar

Only at a level of $p < 0.05$ did we find extra clusters including a cluster with peak MNI coordinate at [-50 -44 40] containing 21 voxels in the left IPL. Another cluster has peak coordinate at MNI-coordinate [40 22 14] containing 12 voxels in the right IFG triangularis and a second cluster with peak-MNI coordinate [44 38 -2] with another 12 voxels in the right IFG triangularis.

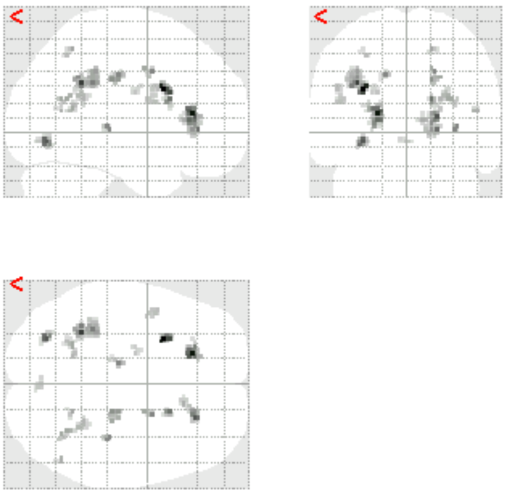

Figure 9: Glass brain showing the cross modal repetition suppression effect for word-unfamiliar at $p < 0.005$

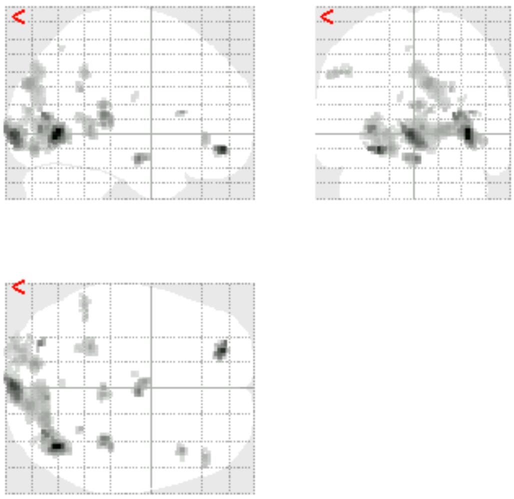

Figure 10: Glass brain showing the cross modal repetition suppression effect for symbol-familiar at $p < 0.05$

Word-familiar

At an uncorrected level of $p < 0.01$ we found a cluster of 15 voxels with a peak at MNI-coordinate [-40 -38 46] in which 9 voxels are in the left IPL, another cluster with peak MNI-coordinate at [34 -44 20] consisting of 281 voxels of which 8 voxels were in the right IPL. A cluster of 13 voxels contains 9 voxels in the right IFG opercularis and has peak MNI-coordinates at [40 14 12].

Symbol-unfamiliar

At uncorrected $p < 0.005$ we see a CMRS effect in a cluster of 11 voxels with peak MNI-coordinate [-46 -46 26] containing 5 voxels in the left IPL. Also we see the cluster with peak MNI coordinate at [58 28 0] that we found at $p < 0.001$ again at the $p < 0.005$, only now the cluster is 142 voxels big and contains 141 voxels in the right IFG of which 130 in the IFG triangularis. At peak MNI coordinate [-24 32 -12] we find a cluster of 17 voxels of which 11 are located in the left IFG. At peak MNI coordinate [-46 26 -16] another 5 voxels are clustered with 4 voxels in the left IFG as well. Finally, a very big cluster of 759 voxels with peak MNI coordinate at [-12 34 -12] which contains another 6 voxels in the left IFG.

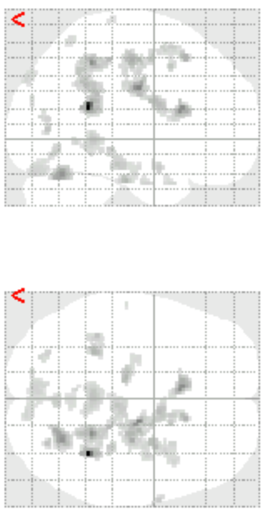

Figure 11: Glass brain showing the cross modal repetition suppression effect for word-familiar at $p < 0.01$

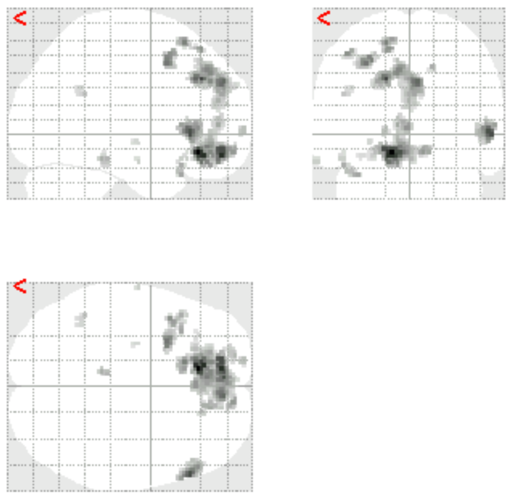

Figure 12: Glass brain showing the cross modal repetition suppression effect for symbol-unfamiliar at $p < 0.005$

In which areas were the voxels located that were ignored for this analysis?

Mostly (>60%) white matter, sub gyral and sub lobar, but also temporal lobe, occipital lobe, supramarginal gyrus, superior parietal lobule, precuneus, superior temporal gyrus, corpus callosum, fusiform face area, insula, middle frontal gyrus, medial frontal gyrus, superior frontal gyrus, precentral gyrus, cerebellum, superior motor area, angular gyrus.

Activated voxels in gray matter

Table 3: summary of exploratory results. The number of voxels that was active in the regions of interest when the significance threshold was lowered to include about 1500 activated voxels per block.

	Left IPL	**Right IPL**	**Left IFG**	**Right IFG**	**Significance level**
Word-unfamiliar	30 voxels	-	14 voxels	-	P < 0.005
Symbol-familiar	21 voxels	-	-	24 voxels	P < 0.05
Word-familiar	9 voxels	8 voxels	-	9 voxels	P < 0.01
Symbol-unfamiliar	5 voxels	-	21 voxels	141 voxels	P < 0.005

4. Discussion

Mirror neurons have been discovered in the macaque brain almost 20 years ago (di Pellegrino et al., 1992), but still a lot is unknown about the MNS in macaques and humans. We hoped to shed light on the question whether mirror neurons are, besides transitive movements, also involved in the processing of intransitive actions. Dinstein et al. (2007) and Lingnau et al. (2009) did not manage to show CMRS evidence for intransitive actions. While other research shows that there is reason to expect CMRS for intransitive actions just as well (Dapretto et al., 2006; Fadiga et al., 1995; Fazio et al., 2009; Iacoboni et al., 1999; Iacoboni et al., 2001; Jackson et al., 2006; Koski et al., 2003; Koski et al., 2002; Maeda et al., 2002; Oosterhof et al., 2010; Patuzzo et al., 2003; Pazzaglia et al., 2008).

By making a distinction between actions labeled by words and actions labeled by symbols and also by making a distinction between actions that are familiar (meaningful) and actions that are unfamiliar (meaningless), we wanted to show that there is CMRS for either actions labeled by words or for familiar actions and not for actions labeled by symbols and unfamiliar actions which would explain the lack of findings in the studies by Dinstein et al. (2007) and Lingnau et al. (2009).

When actions labeled by a word show CMRS and actions labeled by symbols do not, than previous studies (Chong et al. 2008; Kilner et al. 2009) might not have shown mirror neuron responses but merely the activation of verbalizing the actions that were executed and observed. When familiar actions show CMRS and unfamiliar actions do not, than this would show that it is necessary for the MNS that the intention of an action is known.

The whole brain analysis by block showed no significant results at uncorrected $p < 0.001$ for the expected conditions where actions labeled by words were involved and familiar actions. Instead we did find a significant CMRS result in the block symbol-unfamiliar in the right IFG triangularis.

Also the ROI analysis we did to test whether there were significant differences between our two distinctions showed no significant results. Actions labeled by words did not show a significant difference in CMRS effect compared to actions labeled by symbols. Familiar actions also did not show a significant difference in CMRS effect compared to unfamiliar actions.

Thus we could not show evidence that the MNS needs actions to be labeled by words in order to be activated for intransitive actions and also no evidence can be given that the MNS needs to know the action's intention to be activated.

A control block was added to the study for which repetition suppression should arise because all actions in this block were executed and thus we stayed in a single modality and thus the same neurons should become active for repetitions. In this block we saw only significant RS activation in the left IFG. With an $p < 0.001$ we should see approximately 50000*0.001=50 voxels as false positives and we only got 80 activated voxels in total in the EE-block, which makes it difficult to count the CMRS effect in the right IFG as significant. Also the block symbol-familiar only showed nine voxels with a CMRS effect, which does not even come close to the number of false positives we expect to see. So maybe the threshold $p < 0.001$ is too strict for our data.

Because the EE-block raised questions in reaching significance, we decided to explore the data a little further by lowering the significance threshold until the data showed about 1500 activated voxels throughout the brain. This exploration showed CMRS activation in the left IPL for all four blocks, in the right IPL only for word-familiar, right IFG for symbol-familiar, word-familiar and symbol-unfamiliar, and the left IFG for word-familiar and symbol-unfamiliar (see table 3).

The exploration showed us that there might be CMRS activation for all conditions and thus for intransitive actions. For instance if we look at the results for the left IPL, we can show with some calculations that the result is probably significant. When you look at the chance of two events happening at the same time, you have to multiply the chance levels with each other. In the case of the left IPL four events happened at the same time. So by multiplying the chance of false positives of the separate events we can come to the chance of a false positive for all events together, e.g. 0.005*0.05*0.01*0.005=1.25e-08. But we have to control for multiple comparisons because in essence we do four whole brain analyses now. A brain has a volume of 1350 cm^3 and we applied a voxelsize of 3x3x3.5 mm, then 1350/0.0315=42857 voxels fit in a full brain volume. So if we assume one brain volume contains 50000 voxels we do a test on 200000 voxels. The chance of finding a false positive is now the chance of a false positive multiplied by the number of voxels. So for the left IPL we expect to find 0,0025 voxels that do not show a real effect, which is less than one, so all voxels in the left IPL are expected to be true positives.

We can do this calculation for the other locations as well. For the right IFG we have three events, so 150000*2.5e-06=0.375 voxels false positive, so the right IFG probably also shows significant CMRS activation. For the right IPL 500 false positives are expected, so the right IPL does not show a significant CMRS effect. For the left IFG 2.5 false positives are expected, so this is not as strong as the results for the left IPL and the right IFG, but there are more than 2.5 voxels active for left IFG so maybe this is also significant.

We did not find significant differences between the conditions. This could mean that there can be either no CMRS effects for intransitive actions or there could be CMRS effects for all conditions. The exploratory analysis shows evidence for CMRS effects for all conditions and thus that all intransitive actions might show CMRS. Unfortunately, we could not show this effect on the accepted significance level of $p < 0.001$ so no real conclusions can be taken from our results except that more research is needed.

A possible reason for not finding significant results is the movement of the participants. They had to execute hand gestures during scanning, which causes that the brain displaces throughout the scanning period. In preprocessing a correction is applied to avoid movement artefacts in the data, but this is never perfect, you still end up with more noisy data when the participant moved more.

Furthermore, there could be individual differences that had an effect on the data. For instance the dominant hemisphere can be different for the participants. We did not check hemisphere dominancy for participants. Also we morphed all brains to the same standardized brain, but that does not secure that all brain structures are superimposed correctly between participants. It is possible that the CMRS effect was displaced a few millimeters between participants, than the effect would be blurred and might not reach significance.

Another reason for not finding significant CMRS results for intransitive actions could be that there are less neurons specialized for intransitive actions in the brain than for transitive actions. Studies on mirror neurons in the macaque brains show consistently that some actions have more dedicated neurons, than other actions (di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Ferrari, Gallese, Rizzolatti & Fogassi, 2003; Kohler, Keysers, Umilta, Fogassi, Gallese & Rizzolatti, 2002; Rizzolatti, Camarda, Fogassi, Gentilucci, Luppino & Matelli, 1988; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). For instance, the action 'grasping' makes up to fifteen times more neurons fire, than the action 'holding' (Gallese, Fadiga, Fogassi & Rizzolatti, 1996).

The lack of significant findings in the ROI analysis can be due to a bad selection of voxels for the ROI. We used the execution-execution (EE) Block as a localizer for the execution-observation (EO) blocks, but Kilner et al. (2009) showed that the location for the repetition suppression effect for EE trials in the IFG were located 6 mm more lateral than the repetition suppression effect for the EO trials.

There has been criticism on the repetition suppression paradigm, but Larsson and Smith (2011) showed that the paradigm works as long as the design of the experiment is balanced so there is no effect of surprise. Our set-up was randomized and counterbalanced so no single action was viewed or executed more than another and they were spread evenly over the trials so no large rows of similar sequences could appear.

A problem with the repetition suppression paradigm is that you cannot be sure whether there really was repetition suppression when you find a significant effect. In fMRI we measure and average over large amounts of neurons. If we see a repetition suppression effect this could be visible because the same neurons are active but attenuated as we expect, but it could also be that a smaller amount of neurons fired the second time. In macaque monkeys they find all sorts of neurons together in the mirror neuron area F5; execution neurons, observation neurons and execution + observation neurons (di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Ferrari, Gallese, Rizzolatti & Fogassi, 2003; Kohler, Keysers, Umilta, Fogassi, Gallese & Rizzolatti, 2002; Rizzolatti, Camarda, Fogassi, Gentilucci, Luppino & Matelli, 1988; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). But also these neurons sometimes show inhibition for observation and excitation for execution and all sorts of combinations of responses are found (Mukamel, Ekstrom, Kaplan, Iacoboni & Fried, 2010). So CMRS research with fMRI is not conclusive. Invasive studies could be a good way to confirm the findings.

To conclude, we showed that there is reason to continue research on the response of the MNS for intransitive actions and that there is probably not a distinction for actions in labeling or meaningfulness. Our study could not show significant findings to prove this, but our exploration does show results that are indicative of CMRS for all types of intransitive actions in our study. If we speculate on this we could say that the MNS might serve the purpose of connecting one's motor pattern to that of others and that this connection is very global and for all types of hand actions including both transitive and intransitive actions, meaningful and meaningless actions, verbalizable and non-verbalizable actions. We speculate that previous studies (Dinstein et al., 2007; Lingau et al. 2009) could not find cross modal repetition suppression for intransitive actions because intransitive actions give a weaker response than transitive actions because less neurons are dedicated to intransitive actions than transitive actions.

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6. Appendix

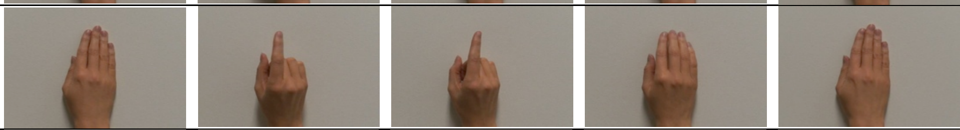
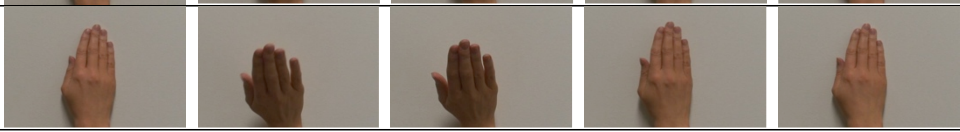
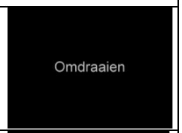
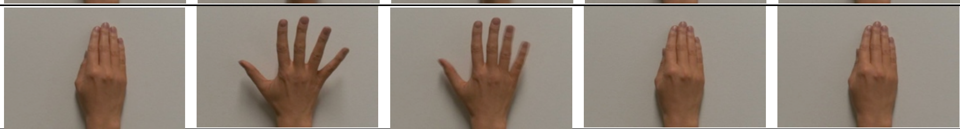
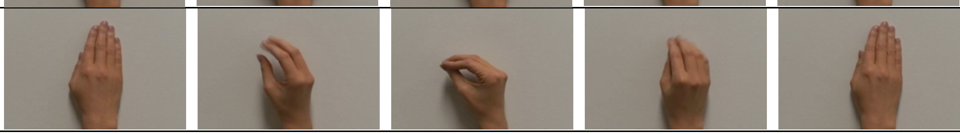
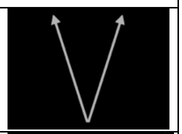
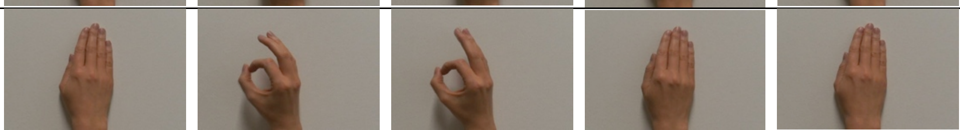
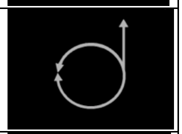
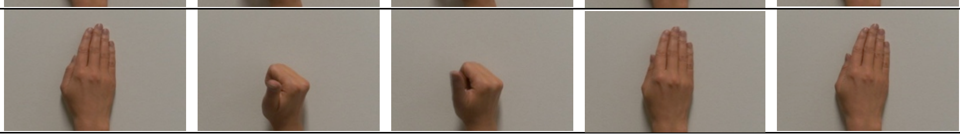
Questionnaire for testing categorization of the actions

Vind je dit een bekend gebaar?	ja	nee	anders, nl:	
Hoe vaak maak je deze beweging zelf?	nooit	soms	regelmatig	vaak
Hoe vaak zie je iemand anders deze beweging maken?	nooit	soms	regelmatig	vaak
Met welk woord zou je deze beweging omschrijven?				

Independent t-tests showed that the meaningful action were significantly more familiar ($t(10)=-6.7$, $p<0.001$). People did the meaningful movements significantly more often ($t(10)=-2.9$, $p<0.05$) and saw the action significantly more ($t(10)=-3.6$, $p<0.05$).

For the attribution of words to the action nice results came out as well. For the word-actions people gave the correct words quite often. Only “groeten” (greet) and “samenbrengen” (bring together) were not so great. Greeting was confused with the stopsign. Later while training the participants it turned out that adding a waving motion to the action would make it more intuitive. Bringing together was just to unfamiliar to people and made people very creative with making words like “duckbeak”, “not quite”, “smaller” or “talk”. The attribution of words to the symbol-actions was not consistent, while the meaning of the meaningful-symbols was consistent. For the six unfamiliar actions no consistent meaning was attributed accept for some correct action descriptions of the hand movement in the cases where the labels were words.

Stimuli

	Stills from video (0 sec, 500 sec, 1000 sec, 1500 sec, 2000 sec)	label
	Word - Familiar	
1		
2		
3		
	Word – Unfamiliar	
4		
5		
6		
	Symbol – Familiar	
7		
8		
9		
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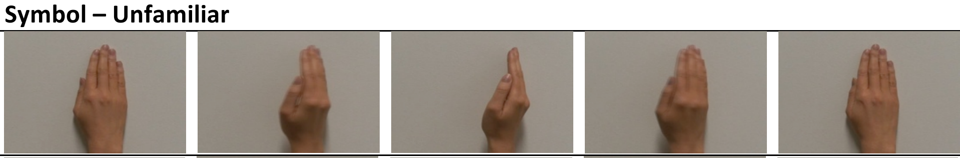
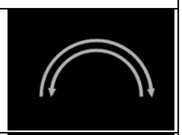
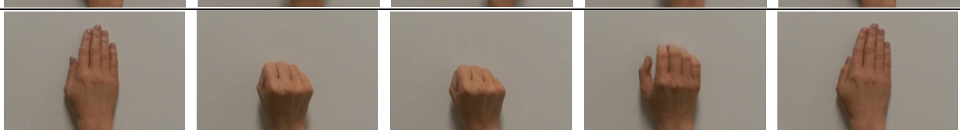
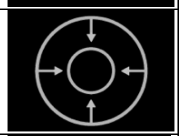
10		
11		
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