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The mirror neuron system and area 46 in the imitation of novel and practised hand actions: an event-related fMRI study

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1.Summary

In Buccino et al. (2004), we found the mirror neuron system (MNS) activated during imitation learning of unfamiliar hand actions (guitar chords). These activations likely reflected the representation of familiar motor elements in the task. During motor preparation, the activity of this circuit was 'orchestrated' by the rostral middle frontal gyrus (BA 46), presumably restructuring these motor elements into a novel finger configuration.

In the present study, we evaluate this restructuring hypothesis by manipulating practice levels on two time scales: expert vs. novice guitarists; and practice with a subset of chords. During action observation (event 1), we observed a complementarity of area 46 and hippocampus: whereas area 46 was only activated for novel chords in the non-guitarists, the hippocampus was activated whenever chords were practised or familiar. During motor preparation (event 2), left area 46, left human AIP, and superior parietal sites bilaterally were activated more strongly for the non-practised chords.

These results indeed indicate a transient involvement of area 46 in imitation learning (restructuring hypothesis).

2. Research questions

	[illegible]	[illegible]
[illegible]	√	√
[illegible]	√	√

1. We sought to replicate the results of our first study that only included non-guitarists and novel chords.
2. According to the restructuring hypothesis, area 46 should be more strongly activated for non-practised than for practised chords.
3. Are practised and non-practised items clearly discriminated during action observation, despite mixed presentation? If so, what is its neural correlate?

3. Method

Sixteen guitarists and 16 non-guitarists participated in the study. All were right-handed and took part in a one-hour practice session with four of the eight chords that were used in the scanning session run one day later.

We ran four scan session of 16 trials each, half of which were motor imagery trials (not reported here). In each session, subjects imitated 4 practised and 4 non-practised items in quasi-random order.

Figure 1 shows the setup in the scanner, and Figure 2 shows the four successive events in each imitation trial.

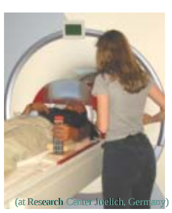


Fig. 1. Experimental setup.

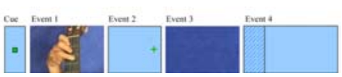


Fig. 2. Event 1: observation of video clip; event 2: prepare exe-cution; event 3: imitate; event 4: rest (baseline).

Events 1 and 2 were presented in jittered durations of 4-10s, event 3 was always 7 s long, and event 4 was jittered over 6-12 s. Functional MR data were acquired with a 1.5T Siemens Sonata scanner with EPI capability (TE = 66 ms, TR = 3 s, flip angle = 90°, FOV = 200 mm, slice thickness 4 mm, 3 x 3 mm in-plane resolution). SPM2 was used for the entire data analysis. For the group analysis, random effects analysis (Friston et al., 1999, NeuroImage) was used ($p_u < 0.001$).

4. Percent Signal Change analyses

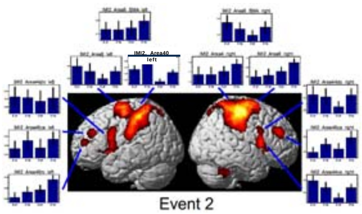
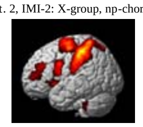


Fig. 3. PSC-results for Event 2 (motor preparation).

For each of the three events, we calculated a contrast map for the simple main effect vs. rest (across groups and practice levels) to identify the task-relevant areas. Then the percent BOLD signal at the related activation peaks was extracted separately for the four conditions and analysed to identify differential activations. E.g., for event 2 as shown above, the related 4-way ANOVA (Group x Area x Practice x Session) revealed a significant effect of Practice, $F(1, 30) = 3.78$, $p < .05$, and a just significant Area * Practice inter-action, $F(11, 330) = 1.82$, $p < .05$. These results guided the selection of the contrasts shown below.

5.1 Results I: Replication (Event 2)

Expt. 2, IMI-2: X-group, np-chords



Expt. 1, IMI-2 (SPM 99)

Expt. 2, IMI-2: M-group, np-chords

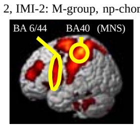


Fig. 4. We could indeed replicate our earlier results (Buccino et al., 2004). Further, non-guitarists (X-group) and guitarists (M-group) showed highly similar activations.

5.2 Results II: Testing the restructuring hypothesis of area 46 (Event 2)

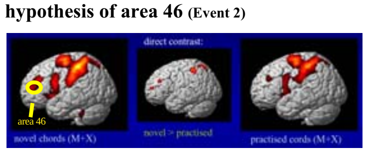


Fig. 5. Basic contrasts for novel and practised intems (both groups).

Imitation of non-practised chords produced stronger activations in left area 46 than for practised chords, as well as in the adjacent, caudal part of the left middle frontal gyrus, in the left posterior parietal cortex (likely human AIP), and in the superior parietal lobe bilaterally.

We propose that area 46 engages in selecting and re-combining the elements represented in PMv and BA 44 to a novel motor pattern (restructuring hypothesis).

Also Rowe et al. (2000, Science, 288) characterised the role of area 46 as selecting representations for execution. In our task, this is likely based on a visuo-spatial representation of the observed finger positions in the two posterior parietal sites (human AIP and SPL).

Fig. 6. A simple way in which restructuring of motor represen-tations in the MNS might be achieved: sequential attending to different visuo-tactile-motor elements (panels a, b, and c) and to their configuration (panel d).

5.3 Results III: Action observation (Event 1)

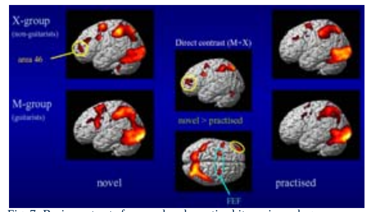


Fig. 7. Basic contrasts for novel and practised items in each group.

During action observation, non-practised items attract enhanced attention, indicated in the direct contrast by stronger activations in posterior parietal sites, frontal eye fields, left area 6/44 and left area 46. As apparent from the basic contrasts, area 46 shows no significant activations for the guitarists, likely due to the fact that also the non-practised chords were familiar to them.

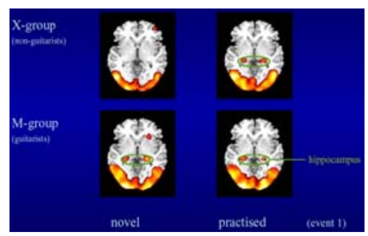


Fig. 8 indicates a neat complementarity between area 46 and hippocampus: the latter is only activated when items are familiar or practised, area 46 only for novel items.

6. Conclusions

How does the brain encode, for subsequent imitation, actions that are not yet in the behavioural repertoire of the observer? Results confirmed that the required perception-action matching relies on the mirror neuron circuit (inferior parietal lobule and posterior part of inferior frontal gyrus, see Fig. 4). However, this motor resonance mechanism is not sufficient for imitation learning. This study confirmed the restructuring hypothesis, according to which prefrontal area 46 is engaged in restructuring familiar motor elements represented in the MNS.

Accordingly, activations in area 46 were only present for novel items during action observation, and more generally for non-practised items during motor preparation (event 2).

As a trend, guitarists showed weaker activations than non-guitarists during action observation, and stronger activations during execution (not shown here).

Regarding research question 3, non-practised chord items indeed attracted enhanced attention. The complementary activations of area 46 and the hippocampus in the present study suggest that the hippocampus is likely involved in the recognition of familiar items.

References

Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H.-J., & Rizzolatti, G. (2004). Neural circuits underlying imitation learning of hand actions: An event related fMRI study. *Neuron, 42*, 323-334.

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