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


1. Summary
In Buccino et al. (2004), we found the mirror neuron system (MNS) activated during imitation learning of unfamiliar hand actions (motor chords). These activations likely reflected the representation of familiar motor elements in the task. During motor preparation, the activity of the 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 complementary area 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
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 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.

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 = 60 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 < 0.001).

4. Percent Signal Change analyses
For each of the three events, we calculated a contrast map for the simple main effects (both groups and practise groups) to identify the task-related activations. Then the percent BOLD signal at the related activations 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. P (F(1, 30) = 3.78, p < .05, and a joint significant Area x Practice interaction. P(11, 330) = 1.82, p < .05. These results guided the selection of the contrasts shown below.

5. Results
5.1 Results I: Replication (Event 2)
These results indeed indicate transient activations of area 46 and the hippocampus in the present study. All were right-handed and took part in a one-hour scanning session run one day later.

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

5.3 Results III: Action observation (Event 1)
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 64/44 and left area 46. As apparent from the basic contrasts, area 46 shows no significant activations for the guitarist, likely due to the fact that also the non-practised chords were familiar to them.

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

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