Neural circuits underlying imitation of novel hand actions:
an event-related fMRI study

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Observation events (1) → **Preparatory pause events (2)** → **Execution / imitation events (3)**

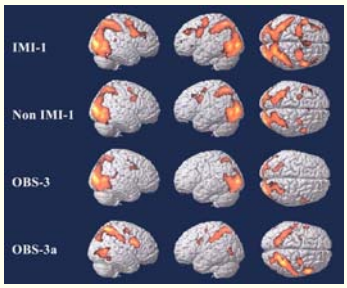


Fig. 1. Cortical areas activated during events in which participants observed a model executing a guitar chord. In the imitation condition, event IMI-1 was directly followed by a preparatory pause (IMI-2, see Fig. 2) and then by imitative execution (IMI-3, see Fig. 3). For the four experimental conditions, see **Figure 5.**

All contrasts are with Event 4 (baseline), except OBS-3a, which is contrasted with Event OBS-1 (observation of guitar neck).

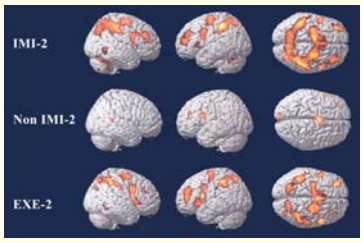


Fig. 2. In the preparatory pause (Events 2, duration 2-8 s), participants prepared execution. In the IMI-condition, this was based on the chord shown during IMI-1. In the Non-Imitation condition, participants also observed a guitar chord during event 1, but they then prepared execution of a simple, non-chord related hand action during Non IMI-2 (note the strong activation decrease). In the EXE condition, participants were not shown a guitar chord during Event 1 but only a moving guitar neck (see Fig. 5). During the subsequent event EXE-2, they were asked to prepare execution of a guitar chord of their choice. Activations in IMI-2 and EXE-2 are very similar.

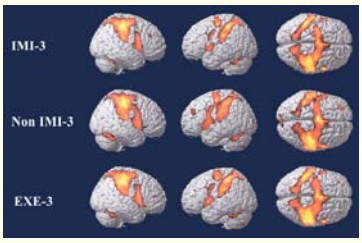


Fig. 3. During IMI-3, participants executed the previously observed guitar chord with their left hand. During Non-IMI-3, they performed a non-chord related hand action, and during EXE-3 they performed a chord of their own choice.

Fig. 4 (right) shows the guitar neck and the screen for display of the model guitar chords.

1. Summary

The neural bases of imitation-based *learning* are virtually unknown. Non-guitarist participants imitated novel, unpractised guitar chords. Event-related fMRI permitted us to separately assess BOLD responses during model observation (IMI-1), motor preparation (IMI-2), and imitative execution (IMI-3). In all phases, we found activations in the same parieto-premotor circuit that is known to be involved in action understanding *(mirror neuron circuit)*. During motor preparation, this circuit is 'orchestrated' by the middle prefrontal cortex *(area 46*, see Fig. 2). We propose that area 46 engages in re-combining the represented motor elements into a complete finger configuration. This extended circuit can either be activated *exogenously* (by a model), or *endogenously* (in the absence of a model) for preparing execution.

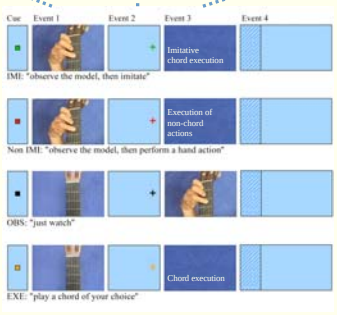


Fig. 5: Experimental design. The 4 conditions are shown in rows, and the 4 successive events of each condition in columns. OBS was a pure observation condition, whereas Events 3 of IMI, Non IMI, and EXE, involved imitative, non-imitative or non-model-guided motor execution. Event 4 was rest (baseline).

2. Method

Twelve right-handed volunteers participated in a 30 min. practice session and the subsequent scanning session. Figure 4 shows the setup in the scanner, and Figure 5 shows the four successive events in the main imitation condition (IMI), as well as in the three control conditions. Guitar chords were presented as video clips during events IMI-1, Non IMI-1, and OBS-3. We ran four blocks of 16 trials each, with quasi-random order of conditions/trials.

Events 1, 2 and 4 were presented in jittered durations of 4-10s, 2-8 s, and 6-12 s, and event 3 was always 7 s long. 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). On average, 37 ± 9 EPI volumes were acquired per event and condition in all participants. SPM99 was used for the entire data analysis. A voxel size of 2 x 2 x 2 mm^3 was used for preprocessing, and data were smoothed with a Gaussian kernel of 10 mm for the group analysis. For the latter, random effects analysis (Friston et al., 1999, NeuroImage) was used ($p_u < 0.001$).

3. Results and Discussion

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 mediation relies on the *mirror neuron circuit* (inferior parietal lobule and posterior part of inferior frontal gyrus). This circuit was active from model observation onwards. During the pause, we also found other structures involved in motor preparation activated (dorsal premotor cortex, superior parietal lobule, rostral mesial areas, see *4. Key* on the right).

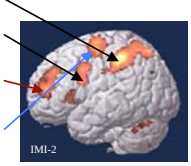
Thus, our results demonstrate that the mirror neuron system also subserves 'true imitation', and not only the imitation of familiar actions as shown previously. However, the transient involvement of *area 46* during the pause indicates that the mirror system is not sufficient for imitation learning. ->

Moreover, we suggest that *area 46* operates as the 'orchestrator' of the mirror neuron system when novel actions need to be combined from elementary motor representations. This interpretation is in line with Rowe et al. (2000, Science, 288) who demonstrated the specific role of this area in response selection, rather than in maintenance in working memory per se. Also the activation of area 46 during EXE-2 that was not preceded by a model supports this.

The direct contrast above confirms that the differences between exogenous (IMI) and endogenous (EXE) activation of the mirror system (s.a. Fig. 2) are small. The stronger activation of the left inferior parietal lobule indicates its role in representing the model.

4. Key: Extended mirror neuron circuit during IMI-2

- inferior parietal lobule (rostral part)
  -> PF; Fogassi et al. (1998); Gallese et al. (2002)
- PMv: ventral part of precentral gyrus / pars opercularis of inferior frontal gyrus
  -> Binkofski et al. (1999); Buccino et al. (2001).
- rostral middle prefrontal gyrus (area 46) -> Rowe et al. (2000, Science)



Additional cortical areas

- PMd: dorsal part of precentral gyrus (preparation of execution-related aspects)
- caudal middle frontal gyrus: (top-down attentional processes ?)
- mesial areas (Fig. 2): pre SMA

(also in all Events 2 and 3 related to chord execution: inhibitory control of mirror circuit; sequencing?)

References *This study was recently published:*

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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