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Research report

Representation of motor habit in a sequence of repetitive reach and grasp movements performed by macaque monkeys: Evidence for a contribution of the dorsolateral prefrontal cortex

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ABSTRACT

In the context of an autologous cell transplantation study, a unilateral biopsy of cortical tissue was surgically performed from the right dorsolateral prefrontal cortex (dlPFC) in two intact adult macaque monkeys (dlPFC lesioned group), together with the implantation of a chronic chamber providing access to the left motor cortex. Three other monkeys were subjected to the same chronic chamber implantation, but without dlPFC biopsy (control group). All monkeys were initially trained to perform sequential manual dexterity tasks, requiring precision grip. The motor performance and the prehension's sequence (temporal order to grasp pellets from different spatial locations) were analysed for each hand. Following the surgery, transient and moderate deficits of manual dexterity per se occurred in both groups, indicating that they were not due to the dlPFC lesion (most likely related to the recording chamber implantation and/or general anaesthesia/medication). In contrast, changes of motor habit were observed for the sequential order of grasping in the two monkeys with dlPFC lesion only. The changes were more prominent in the monkey subjected to the largest lesion, supporting the notion of a specific effect of the dlPFC lesion on the motor habit of the monkeys. These observations are reminiscent of previous studies using conditional tasks with delay that have proposed a specialization of the dlPFC for visuo-spatial working memory, except that this is in a different context of "free-will", non-conditional manual dexterity task, without a component of working memory.

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1. Introduction

A human subject faces for instance the behavioural task to collect strawberries from plants arranged along rows and columns in a garden zone of a few square meters. Although one can pick-up the fruits in a random order without following a systematic spatio-temporal sequence, most people would choose to follow a well-defined sequence (e.g., from top row to

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bottom row and/or from left column to right column or vice-versa). When first confronted to the task, a systematic order in the picking sequence derives from a motor strategy aimed at optimizing the task (e.g., to not miss a few plants, a risk inherent to a random exploration). When the same task is repeated over and over, then the motor strategy turns into a motor habit, in which the subject does not re-think to optimize the task. In this context, it is legitimate to address where such motor habit related to over-trained and nearly automatic sequential motor task is represented in the brain.

There are numerous reports from non-human primate studies emphasizing that motor sequencing of voluntary ocular or arm movements is represented in the mesial part of the motor cortex (in the large sense), in particular in the supplementary motor area (SMA), in both the caudal SMA-proper and the rostal pre-SMA (e.g., Mushiake et al., 1990, 1991; Tanji and Shima, 1994; Clower and Alexander, 1998; Shima and Tanji, 1998, 2000; Isoda and Tanji, 2003, 2004; Sohn and Lee, 2007; Berdyyeva and Olson, 2010). In the behavioural paradigms applied in these studies, the temporal sequence of movements was instructed visually and, in most cases, memorized by the monkeys so that it could be repetitively reproduced, before moving on to another sequence of targets, and so on. Still in monkeys (Barone and Joseph, 1989; Funahashi et al., 1993; Ninokura et al., 2004; Shima et al., 2007; Berdyyeva and Olson, 2010), a fairly comparable representation of motor sequencing was found in the dorsolateral prefrontal cortex (dlPFC). A role played by SMA in the control of motor sequences has also been found in human subjects (e.g., Gerloff et al., 1997; Boecker et al., 1998; Deiber et al., 1999; Lepage et al., 1999; Schubotz and Von Cramon, 2001; Verwey et al., 2002; Van Mier et al., 2004; Bengtsson et al., 2004; Kennerley et al., 2004; Tanaka et al., 2010).

In the monkey and human experiments listed above, the motor sequence was strictly controlled (visual guidance and/or memorized) and, in most cases, highly practiced if not over-trained. Although the sequential task of strawberry picking introduced as example in the first paragraph above may also be over-practiced, it is fundamentally different in the sense that it is a “free-will” motor performance without imposed sequential order. Furthermore, there is neither visual guidance nor memorization (at least in the working memory) of the motor sequence. The neural representation of such motor habit underlying a motor sequence performed mainly automatically is poorly understood. To address this issue, adult monkeys were trained to perform repetitive manual dexterity tasks (derived from previous versions: see Brinkman and Kuypers, 1973; Brinkman, 1984), comprising a spatial component and a temporal sequence, thus possibly implicating dlPFC, at least during the training phase (Shima et al., 2007). Nevertheless, contrarily to most, if not all, studies on dlPFC (e.g., Barone and Joseph, 1989; Ninokura et al., 2004; Shima et al., 2007), which are built on conditional tasks with delay and emphasize on the retention of a pertinent information (spatial) used to execute the sequential task correctly, the present results are based on “free-will” manual dexterity tasks (see Schmidlin et al., 2011). The manual tasks require a sequence of repetitive movements aimed at different locations, in absence of any constraint of success, temporal order or pace. In other words, the motor tasks used in the present study are non-conditional, without delay, thus not implicating working memory per se once learning or practice is acquired. In this context, after a stable motor performance was reached, thus excluding the learning phase, a unilateral biopsy of cortical tissue was performed surgically in the right dlPFC of intact monkeys, with the aim to culture progenitor cells in order to perform subsequently an autologous reimplantation into the lesioned motor cortex (Kaeser et al., 2011). We hypothesized that in such situation of over-trained sequential movements based on motor habit, the lesion of dlPFC was performed at a site that is non-pertinent for the motor control itself (manual dexterity performance), but it remains unclear whether the dlPFC still plays a role in the representation of motor habits governing the sequential order of repetitive manual dexterity movements to be performed to complete an over-trained motor task executed on a “free-will” basis. Addressing this issue for dlPFC is also prompted by a previous observation also in macaques that a lesion of an adjacent cortical area (SMA) led to a change of motor sequence for a similar manual dexterity task (Brinkman, 1984).

Considering dlPFC as a candidate for such motor habit representation is consistent with the multisensory inputs reaching dlPFC and its projections to brain structures with motor functions, such as the premotor cortex, the superior colliculus, and the basal ganglia. Premotor areas, in turn, project to the primary motor cortex and to the spinal cord (Bates and Goldman-Rakic, 1993; Dum and Strick, 1991, 2005; Fang et al., 2006; Kurata, 1991; Leichnetz, 1986; Lu et al., 1994; Matelli et al., 1986; Rizzolatti and Luppino, 2001; Sakagami and Watanabe, 2007). It has been demonstrated that PFC, in particular dlPFC, plays a crucial role in motor learning and in the intuitive optimization of a task (establishment of a strategy), whereas its implication seems to decrease as the task is progressively trained and automated, delegating the responsibility of the realization of this acquired specific motor task to other brain regions, such as basal ganglia, premotor, primary motor, supplementary motor and cingulate motor areas (see for review Hadj-Bouziane et al., 2003; Halsband and Lange, 2006; Passingham, 1996). Nevertheless, one cannot exclude that dlPFC remains engaged in a neural network underlying motor habits adopted to perform a “free-will” sequential motor task.

2. Methods

2.1. Subjects and behavioural tasks

For the present study, data were collected from a group of 5 male long-tailed macaques (*Macaca fascicularis*), weighting between 3 and 6 kg (Mk-VA, Mk-SL, Mk-JA, Mk-JO, Mk-AV). The monkeys ranged from 2.5 to 5.5 years old at the time of initiation of behavioural training sessions. All the behavioural and surgical procedures were approved by the local ethical committee, in accordance with the Guidelines for the Care and Use of Laboratory Animals and approved by Swiss veterinary authorities (see e.g., Kaeser et al., 2010, 2011; Bashir et al., 2012; Schmidlin et al., 2011). Briefly, the monkeys were trained to enter and sit into a Plexiglas primate chair

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