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MODULATION OF LOCAL FIELD POTENTIAL IN THE MACAQUE PUTAMEN DURING A MUTUAL ACTION TASK

MODULAZIONE DEL LOCAL FIELD POTENTIAL NEL PUTAMEN DEL MACACO DURANTE UN COMPITO DI AZIONE MUTUALE

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ABSTRACT (ENG)

The mirror neuron (MN) network is a complex system, composed of several reciprocally interconnected cortical areas, that plays a role in matching the visual description of an observed motor action with a motor representation in the observer's repertoire. Recent anatomical data suggest that also subcortical areas, including the basal ganglia (BG), might contribute to this network. Indeed, the putamen nucleus - the main input station of the BG - receives dense projections from cortical areas representing crucial nodes of the hand MN network. Although the motor role of the putamen is widely accepted, its specific involvement in planning and execution of grasping actions, as well as in motor-based high-order perceptual and social functions, including the encoding others' observed actions, is still poorly understood.

Therefore, the present study aims at investigating the functional proprieties of the macaque putamen during a Mutual Action Task, in which the monkey and the experimenter alternately had to either grasp a multi-affordance object with a precision grip or a whole hand prehension, or to remain still while observing the partner performing the same actions. This task allowed us not only to assess the putamen encoding of one's own and others' action, but also the encoding of specific aspects of action, focusing in particular on the grip type. The approach used to investigate these properties involved the extracellular recording of Local Field Potentials (LFPs), a signal that mainly reflects postsynaptic potentials and that therefore provides information about inputs to an area and local processing.

Our results clearly illustrate that LFPs recorded from the macaque putamen are modulated by both action execution and observation of grasping actions. Specifically, we found that both conditions were associated with a desynchronization of the alpha/beta and the high beta/low gamma bands and with a synchronization of the delta/theta and the high gamma bands. We also found a different modulation of the delta/theta band for the grip type during action execution. Notably, modulations produced by action observation were systematically less marked compared to those produced by action execution, suggesting that partially overlapping but non-identical putaminal networks are active during action execution and observation.

Overall, these data suggest a role of the putamen nucleus in the encoding of one's own and others' observed actions and underpin the hypothesis of the involvement of the BG in the extended MN network.

ABSTRACT (ITA)

Il sistema specchio è un network complesso, composto da diverse aree corticali reciprocamente interconnesse, che ricopre un ruolo chiave nella trasformazione della descrizione visiva di un'azione osservata in una rappresentazione motoria contenuta all'interno del repertorio dell'osservatore. Recenti evidenze anatomiche suggeriscono che anche aree sottocorticali, tra cui i gangli della base (GdB), potrebbero contribuire a questo network. Infatti, il nucleo putamen, principale stazione di input dei GdB, riceve dense connessioni da aree corticali che rappresentano nodi cruciali di questo sistema. Nonostante il ruolo motorio del putamen sia ampiamente accettato, il suo specifico coinvolgimento nella pianificazione ed esecuzione di azioni di afferramento e in funzioni percettive e sociali di alto livello, tra cui la codifica delle azioni altrui, rimane tuttora poco esplorato.

Pertanto, il presente studio ha come obiettivo quello di investigare le proprietà funzionali del putamen del macaco durante un Mutual Action Task, in cui la scimmia e lo sperimentatore devono alternatamente afferrare un oggetto multi-affordance con una presa di precisione o una presa di forza, o rimanere fermi mentre il partner esegue lo stesso tipo di azione. Questo task ci ha consentito non solo di indagare la codifica delle azioni proprie e altrui da parte del putamen, ma anche la codifica di specifici aspetti dell'azione, e in particolare il tipo di presa. L'approccio usato per investigare queste proprietà prevedeva la registrazione extracellulare del Local Field Potential (LFP), un segnale che riflette primariamente i potenziali postsinaptici e che pertanto fornisce informazioni circa il processamento locale e gli input di una struttura.

I nostri risultati hanno evidenziato una chiara modulazione del segnale LFP sia durante l'esecuzione che durante l'osservazione di azioni di afferramento. Nello specifico, abbiamo osservato che entrambe le condizioni erano caratterizzate da una desincronizzazione della banda alfa/beta e della banda beta alta/gamma bassa e da una sincronizzazione della banda delta/theta e gamma alta. Abbiamo anche osservato una diversa modulazione della banda delta/theta per il tipo di presa nella condizione di esecuzione. In particolare, le modulazioni prodotte dall'osservazione dell'azione erano sistematicamente meno intense rispetto a quelle prodotte dalla sua esecuzione, suggerendo che network parzialmente sovrapposti ma non identici vengano attivati durante l'esecuzione e l'osservazione.

Nel complesso, questi dati suggeriscono un ruolo del putamen nella codifica delle azioni proprie e altrui e supportano l'ipotesi di un possibile coinvolgimento dei GdB nel sistema specchio.

1 INTRODUCTION

1.1 The cortical motor system: beyond motor control

For a long time it was believed that perceptual, sensory and motor processes occurred serially in anatomically distinct cortical areas: information arising from sensory regions would be integrated by associative areas and sent to motor areas to make proper movement execution possible (Rizzolatti and Sinigaglia, 2006). Therefore, the motor cortex has long been associated with a merely executive role, as demonstrated by attempts to map body movements on the motor cortex, which resulted in the simiunculus (Woolsey et al., 1952) and the homunculus (Penfield and Rasmussen, 1950), obtained by the electrical stimulation of the surface of monkey and human motor cortex, respectively. However, current knowledge has dramatically changed the view on the anatomo-functional organization of the motor system, highlighting a more complex network of areas involved in several processes that go beyond simple motor control, including motor-based perceptual, cognitive and social functions.

1.1.1 Anatomo-functional organization of the motor cortex

The motor cortex of primates has been more extensively studied in the macaque monkey, where it corresponds to the agranular frontal cortex located in the posterior part of the frontal lobe, rostrally to the central sulcus and caudally to the arcuate sulcus. Initially, based on different cytoarchitectonic features, Brodmann (1909) subdivided the primate motor cortex in two regions separated by the precentral sulcus: area 4, densely populated of large size pyramidal neurons and corresponding to the primary motor cortex (M1 or F1), and area 6, characterized by smaller pyramids and corresponding to the premotor cortex (PMC). More recent anatomical and functional data provided strong evidence that area 6 could been further parcellated in a mosaic of anatomo-functionally distinct areas, each establishing specific patterns of anatomic connections and containing independent body movement representations (Matelli et al., 1985; Kurata and Hoffman, 1994; Rizzolatti et al., 1998). Macroscopically, area 6 contains three main sectors: a mesial region, subdivided in F3 (supplementary motor area, SMA) and F6 (pre-supplementary motor area, pre-SMA), a dorsal region comprising F2 (dorsal premotor cortex, PMd) and F7 (pre-dorsal premotor cortex, pre-PMd), and a ventral region (ventral premotor cortex, PMv), including F4 and F5 (Matelli et al., 1985) (Fig. 1).

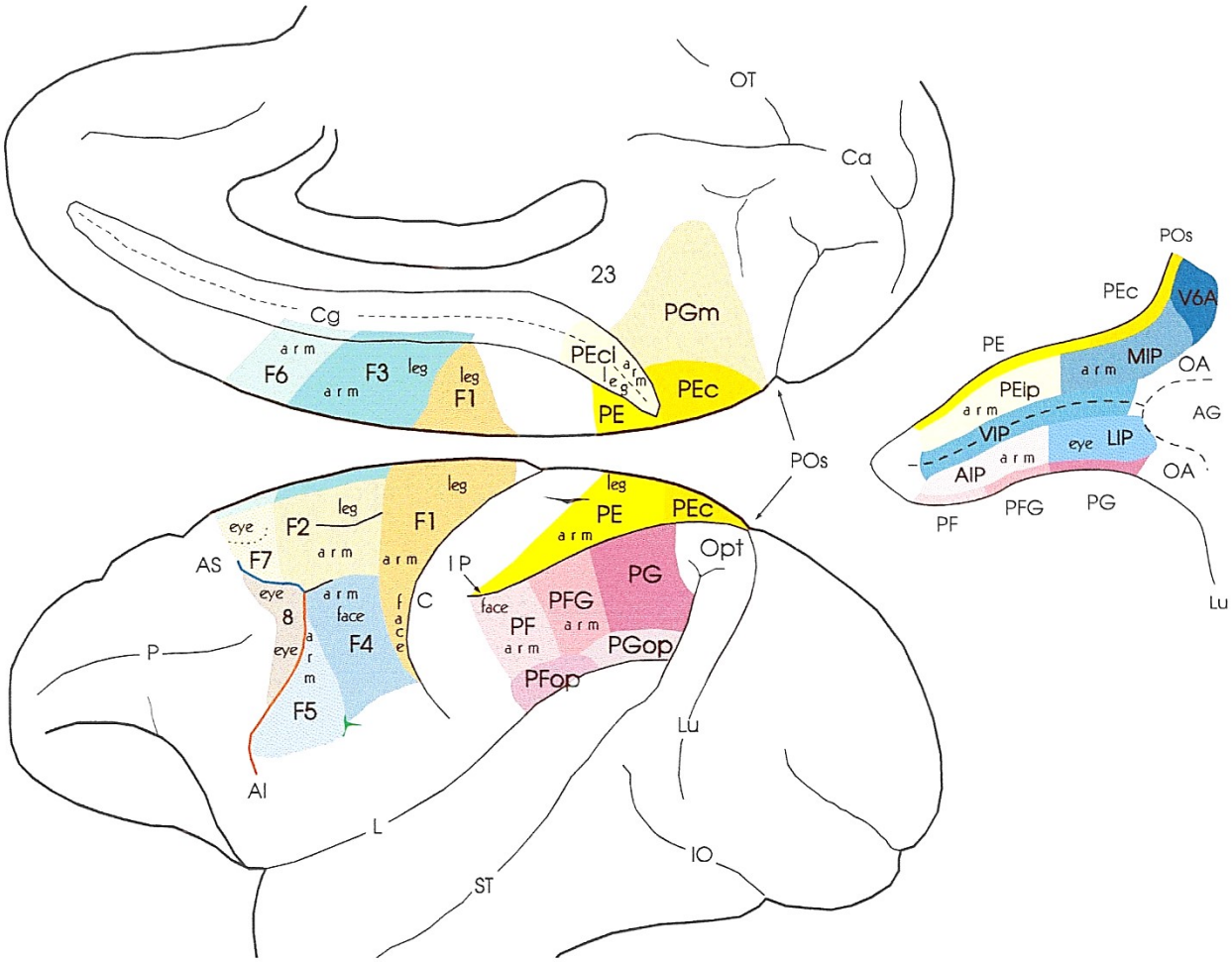


Figure 1 | Organization of the cortical motor system. Mesial and lateral views of the macaque brain, showing the parcellation of the frontal and the parietal lobe and their somatotopic organization. Figure from Rizzolatti et al. (1998)

Areas F1, F2, F3 and parts of F4 and F5 send direct projections to the spinal cord, but while a great portion of corticospinal projection neurons originating from F1 directly terminates on motor neurons, affecting the fine morphology of the executed movement, other premotor areas almost exclusively project to spinal interneurons forming medullar circuits and thus influencing more global aspects of movements. On the other hand, F6 and F7, located in the rostral part of the motor cortex, sends direct descending projections to the brainstem and to other premotor areas, but not to the spinal cord or to F1, exerting a more indirect motor control compared to other motor areas. In addition to descending projections, the motor cortex also establishes direct connections with the parietal lobe (PL), the prefrontal cortex (PFC) and the cingulate cortex (CMA) (Luppino and Rizzolatti, 2000). The rostral premotor areas are richly interconnected with the PFC and the CMA, involved in high-order functions such as motivation, memory and long term plans (Devinsky et al., 1995; Miller, 2000). Caudal areas of the motor cortex, instead, are tightly interconnected with the posterior

parietal cortex, also arranged in a mosaic of areas (Fig. 1) that form a series of largely segregated circuits in which each area of the frontal cortex is related predominantly to a specific parietal area (Rizzolatti et al., 1998).

1.1.2 Parieto-frontal circuits and sensorimotor transformations

Parieto-frontal circuits are involved in sensorimotor transformations, namely the transformation of sensory information about the physical world into pragmatic representations of the opportunities for actions afforded by inanimate objects (Cisek and Kalalska, 2010) and the actions of others (Orban et al. 2021).

Reciprocally interconnected frontal and parietal areas host neurons with similar functional properties: posterior parietal areas, traditionally labelled as 'associative', in addition to neurons with sensory functional properties, also contain neurons discharging in relation to active movements in the dark (Taira et al., 1990; Rozzi et al., 2008); conversely, the motor cortex, historically associated with motor functions, also includes neurons with sensory functional properties (Rizzolatti et al., 1987; Murata et al., 1997).

For instance, area AIP, located in the anterior part of the lateral bank of intraparietal sulcus, contains visuo-motor neurons discharging during both the observation of an object and its manipulation (Taira et al., 1990). AIP establishes direct connections with the sector of F5 located in the posterior bank of the inferior arcuate sulcus (F5a/p) (Matelli et al., 1985; Belmalih et al., 2009) that, in addition to purely motor neurons related to hand movements, also contains visuo-motor neurons with functional properties like those discovered in AIP (Rizzolatti et al., 1987; Murata et al. 1997). These two areas are part of the so called 'lateral grasping network', a circuit involved in the transformation of intrinsic properties of objects, such as size, shape and orientation, into appropriate grasping movements (Borra et al., 2017).

Not only objects, but also others' actions represent relevant information for animals' behaviour: indeed, as well as inanimate objects, observed actions provide affordances, namely opportunities to interact with others (Orban et al., 2021). In this regard, a fascinating class of neurons involved in sensorimotor transformations is represented by some visuo-motor neurons, discovered for the first time in the subdivision of F5 located on the postarcuate convexity cortex (F5c), firing during both the execution of a goal-directed action and the observation of a similar action performed by an experimenter (Di Pellegrino et al., 1992) or a conspecific (Rizzolatti et al., 1996). The exploitation of the same neuronal substrate involved in action planning and execution to represent others' actions led to the use of the term 'mirror neurons' (MNs) to refer

to this class of neurons (Bonini et al., 2022). In addition to F5, neurons with mirror properties were found in the inferior parietal lobule (IPL), and specifically in areas PF and PFG (Gallese et al., 2002; Rozzi et al., 2008), anatomically connected to F5 (Petrides and Pandya, 1984).

A recent finding also suggests the inconsistency of a dichotomous view that sees the encoding of observed actions as separate from that of inanimate objects: the existence, in the PMv, of visuo-motor neurons that, in addition to observed actions, were also modulated by the visual presentation of graspable objects (Bonini et al., 2014). Furthermore, object-related responses of these neurons were not purely visual but varied based on the observer's possibility to interact with objects, likewise action observation responses: in fact, most of the neurons responded stronger when objects (Bonini et al. 2014) or other's action (Caggiano et al. 2009; Maranesi et al. 2017) were presented in the peripersonal space, while some other neurons showed selectivity for stimuli presented in the extrapersonal space (Bonini et al. 2014; Maranesi et al. 2017). It has been proposed that space-constrained representations could play a role for planning actions and for preparing behavioral reactions in the physical and social world (Maranesi et al., 2014)

1.1.3 The cortical mirror neuron network

IPL and PMv (including F5) represent two crucial nodes of a more extended network of anatomically connected cortical regions, the mirror neuron (MN) network, matching the visual description of a motor action with its motor representation contained within the observer's repertoire (Fogassi and Ferrari, 2011). This network also include the anterior intraparietal area (AIP) (Pani et al., 2014; Lanzillotto et al., 2019); dorsal and mesial premotor cortex (PMd and PMm) (Livi et al., 2019; Papadourakis and Raos, 2019); primary motor cortex (M1) (Dushanova and Donoghue, 2010); medial frontal cortex, specifically the pre-supplementary motor (pre-SMA) and the anterior cingulate cortex (ACC) (Mukamel et al., 2010; Yoshida et al., 2011). The main source of biological visual information to this system is thought to be the anterior part of the superior temporal sulcus (STSa), which establishes direct connections with IPL but not F5 (Seltzer and Pandya, 1994). Indeed, STSa contains visual neurons responding to the observation of biologically meaningful movements, including specific hand-object interactions, but that unlike MNs, they do not discharge in association with motor behaviour (Perrett et al., 1989). Another possible source of sensory information is the secondary

somatosensory cortex (Hihara et al., 2015), establishing direct connections with both premotor (Gerbella et al., 2011) and parietal areas (Disbrow et al., 2003; Borra et al, 2008) (Fig. 2).

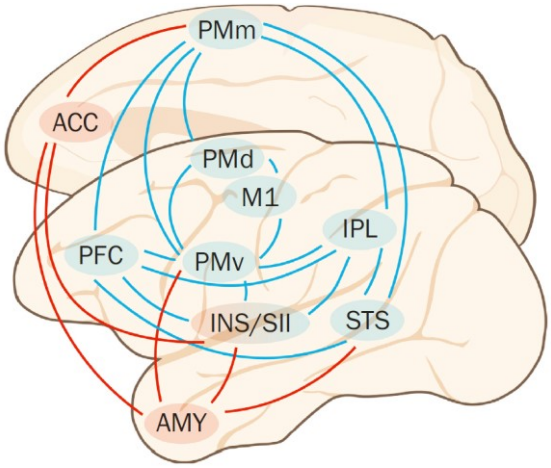


Figure 2 | Organization of the primate MN network. Nodes of the sensorimotor MN network are represented in blue. This figure also includes emotion-related areas (in red) that are thought to be part of the limbic MN network, linked to the mouth/face motor control and involved in communication/emotions and reward processing (for more details, see Ferrari et al., 2017). ACC = anterior cingulate cortex, AMY = amygdala, INS = insula, IPL = inferior parietal lobule, PMd = dorsal premotor cortex, PMm = mesial premotor cortex, PMv = ventral premotor cortex, M1 = primary motor cortex, PFC = prefrontal cortex, SII = secondary somatosensory cortex, STS = superior temporal sulcus. Figure from Bonini et al. (2022)

Using indirect techniques, several studies identified the same action-observation matching system in human (Molenberghs et al., 2012). However, only one study on epileptic patients directly revealed the existence of single neurons modulated by both action execution and observation in the human brain (Mukamel et al., 2010).

Cortical areas forming this network are not isolated, but work in concert with subcortical structures, including the basal ganglia (BG), supporting their functioning. Although the presence of mirror neurons has not yet been directly demonstrated in the BG, several lines of evidence support the idea of the involvement of this structures in the extended MN network (Kessler et al., 2006; Alegre et al., 2010; Caligiore et al., 2013; Gerbella et al., 2016; Bonini, 2017).

Ever since their discovery, MNs have been subject of great interest and heated debates regarding their origin and functions (Casile et al., 2011; Cook et al., 2014). According to the original hypothesis, they might be the neuronal substrate of action recognition and intention understanding (Rizzolatti and Sinigaglia, 2006). More recent perspectives also suggest a possible role in anticipation and prediction of others' behaviours and in the selection of appropriate behavioral responses to observed actions during social interactions (Bonini and Ferrari, 2011; Maranesi et al., 2014; Bonini, 2017). Limited to humans, it has been speculated that the MN

network could be involved in imitation (Molenberghs et al., 2009) and speech perception and production (Rizzolatti and Arbib, 1998). However, to date, none of these functional roles could be demonstrated.

1.2 The basal ganglia

The basal ganglia (BG) complex refers to a symmetrical system of interconnected subcortical nuclei in the forebrain, whose anatomical and functional organization has been conserved throughout vertebrate evolution (Grillner et al., 2013). Through the widespread projections they receive from the cerebral cortex and other brain structures, the BG contribute to several functions, including motor control, motor learning, emotional and cognitive processing.

1.2.1 Anatomo-functional architecture of the basal ganglia

The BG nuclei can be macroscopically organized in three groups: input nuclei, intrinsic nuclei and output nuclei (Lanciego et al., 2012). Input nuclei receive incoming information and project it to intrinsic nuclei. They include the ventral striatum, formed by nucleus accumbens and the dorsal striatum, composed of two nuclei sharing the same embryological origin, namely the caudate nucleus and the putamen. The cerebral cortex and the thalamus are the main source of striatal inputs, with corticostriatal and thalamostriatal projections forming the 85% of all synapsis in the primate striatum (Tepper et al., 2007). Virtually the entire cortex establishes direct connections with the striatum (Kemp and Powell, 1970), whereas thalamic inputs primarily originate from the centromedian (CM) and parafasciular (Pf) nuclei (Sadikot et al., 1992). Other sources of striatal inputs are the substantia nigra pars compacta (SNc), the raphe nuclei and the amygdala (Moore et al., 1971; Parent et al., 1983). Intrinsic nuclei, namely the external segment of the globus pallidus (GPe), the subthalamic nucleus (STN) and the substantia nigra pars compacta (SNc), are relay stations within the BG circuitry. They retransmit signals processed by input nuclei to the output nuclei of the BG, i.e. the internal segment of the globus pallidus (GPi) and the substantia nigra pars reticulata (SNr). GPi and the SNr, in turn, send efferents to the thalamus and the brainstem (Utter and Basso, 2006) (Fig. 3). The main thalamic targets of the BG are the ventral-anterior, ventro-lateral and intralaminar nuclei, which in turn send reentrant projections to the same cortical areas that provided original inputs to the striatum, forming the so called ‘basal ganglia-thalamocortical’ circuits. These circuits contribute to the processing of sensorimotor, associative and limbic information (Alexander et al., 1991). Targets of the brainstem include the pedunculopontine nucleus (PPN) and the superior

colliculus (SC): through connections with the PPN the BG play a significant role in the regulation of locomotion and postural tone (Takakusaki et al., 2003), whereas by means of their projections to SC, the BG control saccadic eye movements (Hikosaka et al., 2000).

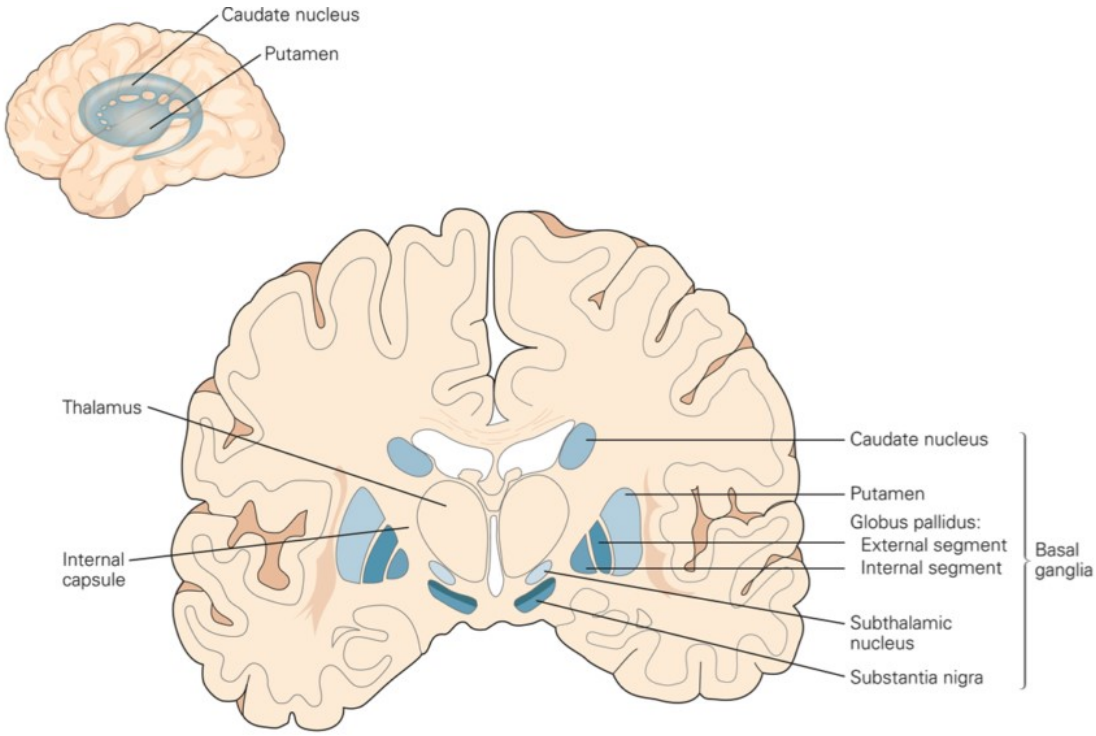


Figure 3 | The basal ganglia nuclei and surrounding structures. The upper left figure is a parasagittal brain section, showing the rostrocaudal extension of the caudate nucleus and the putamen. The lower right figure is a coronal brain section, showing the disposition of the different nuclei. Figure from Kandel et al. (2015)

The vast majority of neurons within the BG nuclei are GABAergic and inhibitory, with the exception of STN, that mainly relies upon glutamatergic excitatory projection neurons, and the SNc, almost exclusively made up of dopaminergic projection neurons (Tepper et al. 2007). Striatal inputs arising from the cortex and the thalamus consist of phasically active glutamatergic excitatory projection neurons (Divac et al., 1977; Galvan and Smith, 2011), whereas nigrostriatal afferents of the SNc are dopaminergic (Moore et al., 1971). The major target of these afferents are the striatal GABAergic projection neurons (Sadikot et al., 1992) (Fig. 4).

The classic model of the functional organization of the BG, proposed by Albin and colleagues in the late 1980s, posits that once processed by the striatum, the signal flows across the circuitry of the BG via two main intrinsic routes: the direct and the indirect pathways. These pathways respectively link directly or indirectly - via the GPe and the STN - the striatum with output nuclei (Albin et al., 1989). The direct pathway

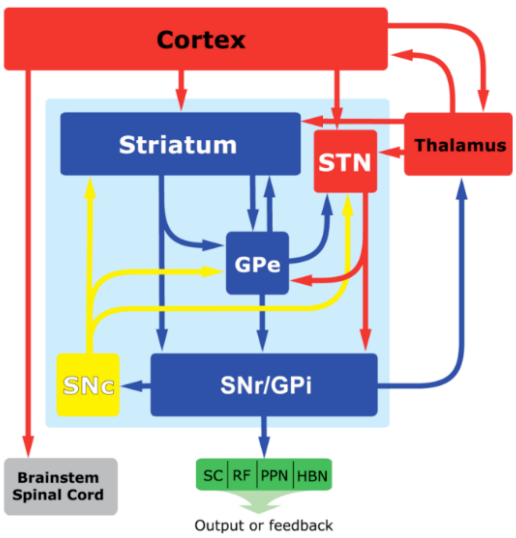


Figure 4 | Neurochemistry of the Basal Ganglia macrocircuits. Nuclei of the BG are included in the light blue. Red indicates structures that are principally glutamatergic, yellow indicates dopaminergic structures, dark blue indicates structures that are mainly GABAergic and green indicates structures with variable neurochemistry. Figure from Tepper et al. (2007)

comprises those striatal GABAergic projection neurons that are directly linked to GABAergic projection neurons of the SNr and GPi. The indirect pathway, on the other hand, comprises striatal GABAergic projection neurons innervating tonically active GABAergic projection neurons of the GPe, linked in turn to glutamatergic projection neurons of the STN (on which they exert a tonic inhibitory influence), which establish connections with GABAergic projection neurons of the GPi and SNr (Tepper et al., 2007). Efferents of the GPi and SNr, consist of tonically active GABAergic neurons, exerting a continuous inhibitory influence upon their targets, the thalamus and the brainstem, that must be temporarily reduced in order to promote their activation. This reduction occurs when the cortex or the thalamus provide an appropriate synaptic drive to striatal neurons (Grillner et al., 2013).

Since output nuclei of the BG receive both inhibitory GABAergic inputs from the direct pathway and excitatory inputs from the indirect pathway, effects of the activation of the two routes on these nuclei are opposite. The activation of the direct pathway results in a temporary inhibition of tonically active GABAergic projection neurons of the GPi and SNr neurons, and consequently in the activation of the thalamus and the cortex. On the other hand, the activation of the indirect pathway tend to suppress the tonically active GABAergic GPe neurons, resulting in a disinhibition of the STN, that in turn increases the excitatory drive on the output nuclei and therefore promote their inhibitory effect upon their thalamic and cortical targets (Alexander and Crutcher, 1990a). Striatal neurons forming the two pathways are also modulated in an opposite way by dopamine released by SNc projecting neurons at the level of the striatum: dopamine facilitates neurons

belonging to the direct pathway, predominantly expressing D1 dopamine receptors, and suppresses indirect pathway neurons, expressing D2 dopamine receptors (Ericsson et al., 2013). The initial model has been expanded including a further pathway, the hyperdirect pathway, which links directly the cortex with the STN, bypassing the striatum (Mathai and Smith, 2011). Thus, besides being a relay nucleus, the STN also represents an input station of the BG, receiving afferents from the cortex, especially the frontal lobe, i.e., primary motor cortex, premotor and prefrontal areas (Monakow et al., 1978).

Historically, two opposing views concerning how the incoming information is processed within the BG were proposed. According to the 'information convergence hypothesis', inputs from cortical areas converge to the BG, where they are integrated and funneled to the motor cortex through the thalamus in order to control motor outputs (Percheron et al. 1994). The 'parallel-processing' hypothesis, instead, posits the existence of multiple parallel and largely segregated circuits within the BG: information sent by distinct cortical areas is processed by mostly non-overlapping areas of the BG and then resent to the cortex through the thalamus, forming partially closed re-entrant parallel circuits, the so called 'basal ganglia-thalamocortical' loops (Alexander et al., 1986). These circuits are partially closed, since most but not all cortical regions providing inputs to the BG are also the targets of the BG outputs (Smith et al., 1998). From a functional point of view, the meaning of these loops is to allow the cortex to activate a regulation system that affects the same cortical activity that initiated the loop. More recent evidence advocate for an intermediate perspective, which assumes the existence of both parallel processing and information convergence: cortical areas that do not share common functions tend to project to distinct regions of the BG, forming largely independent loops, whereas a certain degree of convergence occurs for those cortical areas with closely related functions (Yeterian and Van Hoesen, 1978; Nambu, 2011). Three main functional networks were identified: the sensorimotor, limbic and associative circuits (Yin and Knowlton, 2006). The sensorimotor circuit, formed by the putamen and its connections with M1, SMA and PMC (Takada et al., 2001), appears to be involved in action selection based on the current context (Yin and Knowlton, 2006). The associative circuit, composed of the caudate nucleus and its projections from prefrontal and parietal association cortices (Reep et al., 2003), is thought to play an important role in attentional processes (Van Vleet et al., 2000) and working memory (Levy et al., 1997). Finally, the limbic circuit, comprising the nucleus accumbens and its inputs from the PFC (Montaron et al.,

1996), is assumed to be involved in the selection of final and means-to-end goals based on motivation and reward processing (Corbit and Balleine, 2011; Mannella et al., 2013) (Fig. 5).

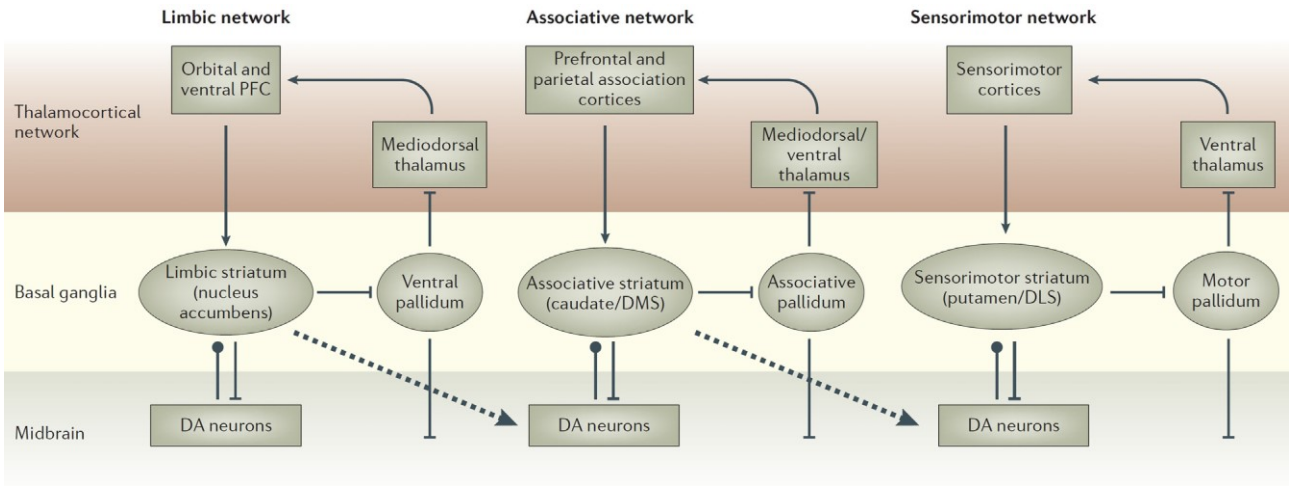


Figure 5 | Main functional networks of the Basal Ganglia. Simplified representation of the three main cortico-striatal regions and their interconnections. Standard arrows indicate excitatory glutamate connections. Flat arrowheads indicate inhibitory GABA connections. Dot arrowheads indicate dopaminergic connections whereas dashed arrows indicate cross-loop connections. Figure from Yin and Knowlton (2006).

Summarizing, given their architecture and functional organization, composed of direct and indirect pathways and parallel and mostly segregated loops, the BG appear to be configured for selection processes (Florio et al., 2018). Within the motor domain, this selection is implemented by two mechanisms: the facilitation of an intended movement and the simultaneous inhibition of competing alternatives (Mink, 1996; Hikosaka et al., 2000). According to the center-surround cooperation hypotheses, while the direct pathway activates specific "central" cortical representations, either the hyperdirect (Nambu, 2004) or the indirect pathway (Mink, 1996) inhibits "surrounding", i.e. competitive representations. However, several other hypothesis about the potential interaction pattern between pathways have been formulated (for details, see Schroll and Hamker, 2013). Dopamine release on striatal neurons also appears to play an important modulatory role in this process increasing the signal-to-noise ratio, and thus enhancing the effects of powerful inputs and reducing the effects of weaker ones (Nicola et al., 2004). Besides the motor domain, this selection process might be extended to other functions, including decision making (Ding and Gold, 2010), error-detection (Schultz and Dickinson, 2000), attention (Ravizza and Ivry, 2001), stimulus-response association and habit formation (Graybiel, 1998; Yin and Knowlton, 2006).

Based on connectional data and functional evidence from human studies, it was also recently proposed that the BG might contribute to the extended MN network (Caligiore et al., 2013; Bonini, 2017). From an anatomically point of view, the BG are tightly interconnected with areas belonging to the lateral grasping network (Gerbella et al., 2016) that, notably, also represent pivotal nodes of the cortical MN for hand actions. Indirect evidence in support of the involvement of the BG in this network also comes from a functional human study (Kessler et al, 2006): investigating the time course of long-range cortical synchronization during an imitation task, authors observed an involvement of the BG in the early stage of processing of biological movements, proposing their possible role in the selection of motor programs matching the observed actions. In light of those findings, Bonini (2017) proposed that the BG might be at the basis of a mechanism that decouples the MN activity from the motor output, in order to prevent the automatic reproduction of observed actions. According to this hypothesis, corticostriatal neurons with mirror properties should be preferentially linked to neurons of the BG belonging to the indirect and/or hyperdirect pathways, whose activation during action observation would result in a suppression of thalamo-cortical output, and thus in an automatic movement suppression. Subsequent fMRI studies revealed a modulation of putamen activity during the observation of hand-object interaction actions (Ge et al., 2018) and an overlapping activation of the STN and the GP during both the observation and execution of manipulative actions (Errante and Fogassi, 2020).

Further evidence of a possible role of the basal ganglia in the MN network comes from comparative studies on songbirds (Prather et al., 2008; Mooney, 2014): the avian area X, which shares strong similarities to the mammalian BG, receives direct inputs from auditory-vocal mirror neurons of the HVC nucleus. These neurons display nearly identical pattern of discharge when the songbird sings a certain vocal sequence and when hears the same sequence (Prather et al., 2008). Furthermore, they do not influence motor outputs, rather receiving an efference copy of downstream motor signals to be matched with incoming auditory input, forming a circuit involved in song learning and categorical perception (Mooney, 2014).

1.2.2 The putamen nucleus

The putamen nucleus forms with the caudate nucleus the main input station of the BG, the striatum. At a macroscopic level, the striatum is a nonlaminar and structurally hetereogeneus complex, formed by two compartments, the striosomes and the matrix, differing in their expression of neurochemical markers and in

input and output anatomical connections (Brimblecombe and Cragg, 2017). Within the striatum, two main types of neurons can be found: projection neurons, covering the 90% of striatal cells, and interneurons, representing the remaining 10% (Lanciego et al., 2012). While interneurons mainly reside in the matrix and at striosomal borders (Aosaki, 1995), both projection neurons of the direct and indirect pathway reside in the matrix as well as in the striosomes (Fujyama et al., 2011).

1.2.2.1 Neurophysiology

From a morphological point of view, striatal projection neurons are classified as medium spiny neurons (MSNs), because of their medium sized cellular spine-free somata and the high density of dendritic spines on distal dendrites (DiFiglia and Pasik, 1976). MSNs have long axons with many collaterals that exit the striatum, as demonstrated by intrasomatic horseradish peroxidase (HRP) injection studies (Preston et al., 1980). Relative to their physiological features, MSNs show a phasic bursty firing pattern, and therefore can be classified as phasically active neurons (PANs): most of them are spontaneously silent and those having a spontaneous firing pattern show a very low discharge rate (Wilson and Groves, 1981). Both extrinsic and intrinsic afferents modulate MSNs activity: extrinsic afferents include cortical and thalamic glutamatergic excitatory neurons and dopaminergic neurons of the SNc (MSNs express high levels of dopamine receptors D1 and D2), whereas intrinsic afferents consist of striatal interneurons and axonal collaterals from other MSNs (Gerfen, 1988). When activated, MSNs temporarily inhibit GABAergic tonically active neurons of the GPe, GPi and SNr (Somogyi and Smith, 1979; Chang et al., 1981; Gerfen, 1988).

The other class of striatal neurons, the interneurons, comprises several types of neurons, including tonically active neurons (TANs) and fast spiking interneurons (FSIs). TANs are large aspiny cholinergic neurons showing a spontaneous irregular firing pattern (Wilson et al., 1990; Aosaki et al., 1995; Apicella, 2002), whereas the FSIs are continuously active GABAergic cells firing at extremely high frequencies (Berke, 2011). Both types of cells modulate MSNs excitability and are in turn under dopaminergic control (Akins et al. 1990, DiFiglia, 1987, Berke, 2011).

1.2.2.2 Connectivity and somatotopy

The most important source of putaminal inputs is the cortex, with both ipsilateral and contralateral afferents arising from nearly the entire cortex (Kemp and Powell, 1970). These projections spread along the entire

rostro-caudal extent of the putamen, but while sensorimotor cortices are mainly related to the postcommissural (caudal) putamen, which is considered the motor territory of the nucleus (Künzle, 1975, 1977; Flaherty and Graybiel, 1991), association areas are preferentially linked to the precommissural (rostral) putamen and to the caudate nucleus (Künzle, 1977).

Sensorimotor cortical areas projecting to the putamen include MI, SMA, PMv and PMd (Takada et al., 1998), Pre-SMA (Inase et al., 1999), CMA (Takada et al., 2001) and SI (Künzle, 1977). Similarly to the these areas from which it receives inputs, the postcommissural putamen nucleus is somatotopically organized and contains at least two distinct body maps, largely segregated mediolaterally and arranged somatotopically in a dorsoventral manner (Romanelli et al., 2005).

Corticostriatal projections arising from M1 are mainly related to the ventrolateral portion of the putamen, whereas those originating from the SMA terminate in a medial and slightly dorsal putaminal sector. A certain degree of overlapping between projections of these two areas exists in the mediolateral central zone. Concerning the somatotopic organization, the hindlimb, forelimb and orfofacial regions of both M1 and SMA project respectively to the dorsal, intermediate and ventral sector of the putamen (Takada et al., 1998) (Fig. 6). Motor representations of the hand originating from frontal areas appear to be located in the same putaminal region targeted by the hand representing area of the primary somatosensory cortex (SI), and the same convergence has been demonstrated for the distal forelimb (Künzle, 1975; Jones et al., 1977).

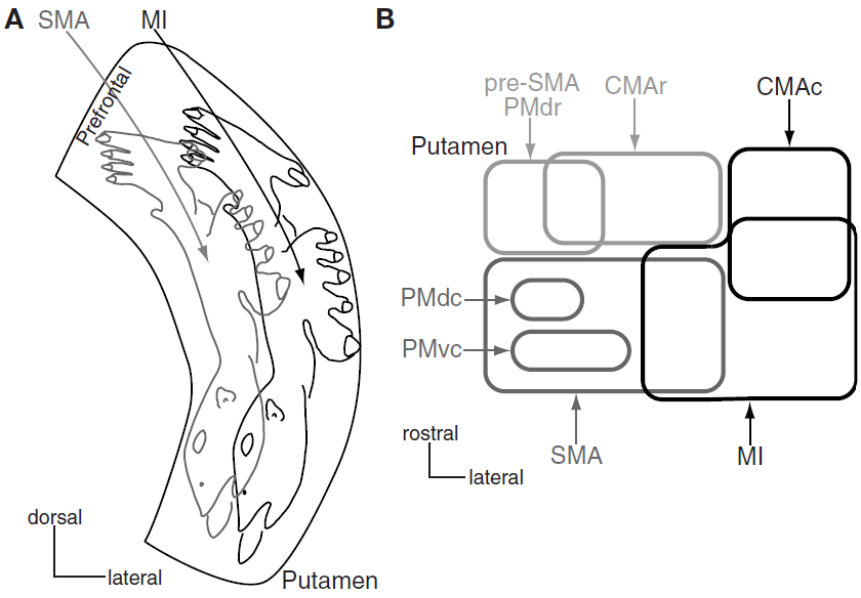


Figure 6 | Somatotopic organization of the putamen. (A) Frontal section of the somatotopy of the putamen. Drawings in black lines represent inputs from the MI, terminating in the ventrolateral putamen, whereas those in gray lines represent inputs from the SMA, terminating in the dorsomedial putamen. (B) Horizontal section of putaminal inputs arising from motor cortices. Figure from Nambu et al. (2011)

This topography was confirmed by physiological studies on nonhuman primates (Alexander and DeLong, 1985; Nambu et al., 2002a). Stimulating forelimb regions of M1 and SMA, Nambu and colleagues (2002a), evoked the orthodromic activation of largely segregated populations of neurons located respectively in dorsomedial and ventrolateral sectors of the putamen. Directly microstimulating the primate neostriatum, Alexander and DeLong (1985) found several striatal microexcitable zones (SMZs) within the putamen, but not the caudate nucleus, that produced movements of different parts of the body. These SMZs were organized in a dorsolateral to ventromedial topography of representations from the hindlimb to the face, with the forelimb represented in an intermediate region. The same somatotopically organized pattern of neuronal activity was observed during both active and passive movements. Using intracortical microstimulation Tokuno and colleagues (1999) identified within the forelimb region of the putamen a further subdivision, with a mediodorsal zone representing the proximal forelimb (elbow and shoulder) and a ventrolateral zone representing the distal forelimb (wrist and digits).

In addition to M1 and SMA projections, the postcommissural putamen receives somatotopically-organized inputs from other cortical motor areas, including PMd, PMv and caudal CMA. The forelimb region of PMd and PMv send projections to distinct portions of the putaminal forelimb SMA recipient zone, respectively to the dorsal and to the ventral sector (Takada et al., 1998). Caudal CMA, on the other hand,

projects somatotopically to a putaminal region that largely overlaps with the M1 recipient zone (Takada et al., 2001).

The putamen nucleus also establishes direct connections with cortical areas forming the "lateral grasping network", subserving the control of purposeful hand actions. In addition to PMv, this network includes IPL and VLPF, involved in the processing of higher order aspects of motor control. PMv, IPL and VLPF projections partially overlap in two putaminal zones, a rostral and a caudo-ventral region (Fig. 7) (Gerbella et al., 2016). Notably, these areas also represent pivotal nodes of the cortical MN network for hand actions: the presence of dense anatomic connections between these cortical regions and the putamen corroborate the hypothesis of the involvement of the BG, and specifically the putamen, in an extended cortico-subcortical MN network (Caligiore et al. 2013; Bonini et al., 2017).

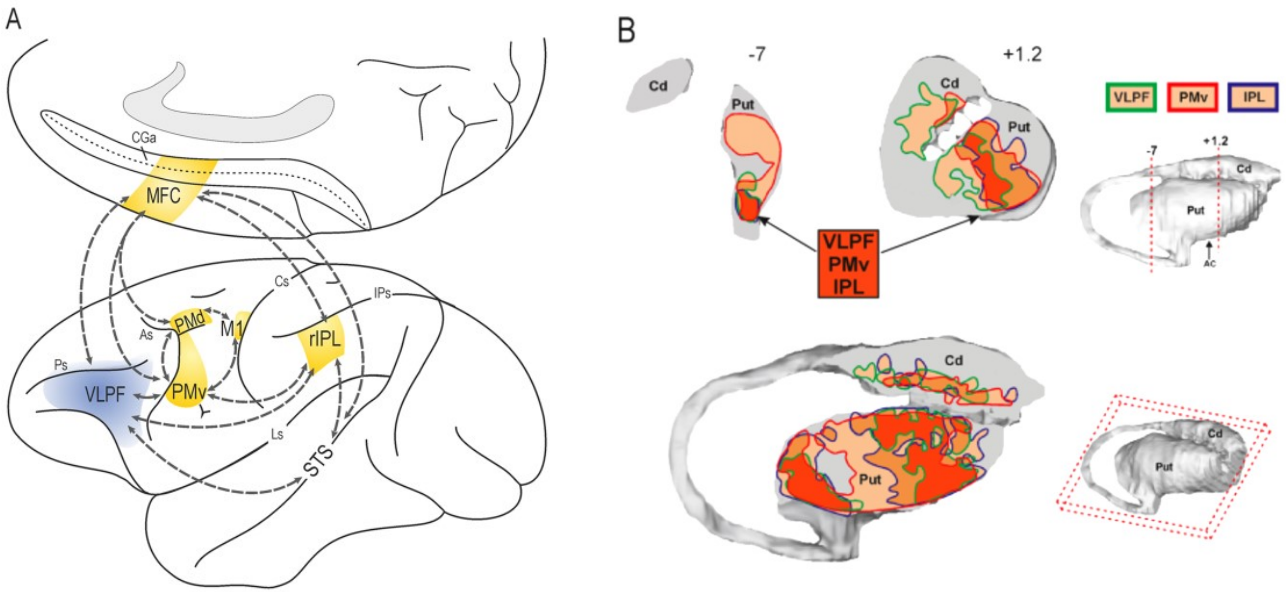


Figure 7 | The extended MN network and its connections with the putamen nucleus. (A) Areas forming the extended MN network: ventrolateral prefrontal cortex (VLPF), dorsal premotor cortex (PMd), ventral premotor cortex (PMv), primary motor cortex (M1), rostral inferior parietal lobule (rIPL) and medial frontal cortex (MFC). (B) Territories of the basal ganglia (BG) receiving projections from the areas belonging to the cortical MN network, namely, PMv (sector with red borders), IPL (blue borders), or VLPF (green borders). The light and dark orange shadings highlight the BG sectors in which two or even all of these three distinct sources of corticostriatal projections overlap. Figure from Bonini (2017).

The second largest source of putaminal inputs is the thalamus, providing projections from parafascicular (Pf), centromedian (CM) and ventral tier nuclei (ventro-anterior and ventro-lateral), which are in turn related to with frontal cortical motor areas: interconnected cortical motor areas and thalamic nuclei send convergent projections to the same region of the putamen (François et al.1991; McFarland and Haber, 2000). Since ventral tier nuclei also retransmit BG outputs to the same motor areas that provide inputs to the

sensorimotor loop (MI, SMA, PM and CMA), it is likely that thalamo-striatal projections provide a positive feedback to the loop, reinforcing circuits underlying a selected behavior (McFarland and Haber, 2000).

Finally, the putamen receives topographically organized inputs from the dopaminergic projecting neurons of the SNc, with lateral parts of this region related to the dorsal putamen and medial parts related to the ventral putamen (Carpenter and Peter, 1972).

With respect to the outputs, the putamen sends topographic projections to specific regions of the GPi/SNr and GPe neurons (Johnson and Rosvold, 1971; Parent et al., 1983). Indeed, besides the putamen, each further step of the BG is organized in a somatotopic manner, and the same is true for the thalamus: this organization suggests that signal related to distinct body parts is processed segregatedly and independently throughout the basal ganglia-thalamocortical sensorimotor loop (Oliveri, 2018). On the other hand, convergence in projections arising from anatomically distinct but functionally-related motor areas suggests an integration of distinct aspects of motor control at the level of the putamen nucleus, such as motor learning and movement execution (McFarland and Haber, 2002; Nambu, 2011).

1.2.2.3 Functional properties and possible functional roles

Traditionally, the putamen nucleus has been assumed to be primarily a motor structure. Several electrophysiological studies demonstrated a correlation between changes in the activity of putaminal neurons, especially PANs, and active and passive movements of specific body parts (DeLong, 1973; DeLong and Strick, 1974; Crutcher and DeLong, 1984; Kimura, 1990). Movement-related neurons located in the distinct sectors of the putamen are modulated by different aspects of movements and motor tasks. The activity of neurons of the lateral putamen, receiving inputs from M1, is related to simple movements, closely resembling that of agonistic muscles (Liles, 1983), and tend to occur at the movement onset (Kimura, 1990), suggesting that these neurons could possibly contribute to the initiation and control of ongoing movements. On the other hand, the activity of neurons of the medial putamen, receiving inputs from SMA, is more related to complex movements (Ueda and Kimura, 2003) and tends to precede movement onset, starting in the post-instruction preparatory interval, after the presentation of a sensory stimulus (Alexander and Crutcher, 1990b; Gardiner and Nelson, 1992). It has been proposed that these latter cells might be involved in the visuospatial organization and temporal structuring of multiple movements for goal-directed actions (Alexander and Crutcher, 1990b; Ueda

and Kimura, 2003). Supporting this hypothesis, some of these set-related neurons are selective for the direction of the forthcoming planned movement (Alexander, 1987) or the spatial location of targets (Alexander and Crutcher, 1990c). However, the data presented above are only correlational: in addition to intracortical microstimulation studies mentioned in the previous section (Nambu et al., 2002a; Alexander and DeLong, 1985; Tokuno et al., 1999) other direct evidence of the involvement of the putamen in motor functions comes from lesional studies. A focal disinhibition of the postcommissural putamen following the injection of the GABA antagonist bicuculline results in stereotyped motor tics (McCairn et al. 2009) and dystonia, which consists in prolonged spasm and abnormal postures (Yamada et al., 1995). A consistent decrease in the putaminal activity is also observed in Parkinson's Disease patients (Wang et al., 2018).

The putamen might also be involved in associative learning and reward-related processes, which appear to be preferentially subserved by TANs: Kimura (1984; 1986) identified some putaminal TANs temporarily suppressed during the presentation of a sensory stimulus, but only if it was repeatedly associated with reward delivery. Aosaki (1994) achieved similar results, also demonstrating that the responsiveness of these TANs was progressively acquired during the operant conditioning. Thus, these neurons appear to process behaviorally significant events and reward prediction (Vicente 2012).

Finally, the putamen could have a role in the integration of visual information and motor representations. Kimura (1986) observed a subclass of PANs exhibiting phasic discharges before the first movement of a repetitive sequence of movements triggered by sensory stimuli, but not before later movements. According to the author, these cells might not be considered neither purely motor nor sensory, but might participate in sensorimotor associations. An fMRI study on healthy human subjects also revealed a modulation of the putaminal activity during the observation of grasping videos, both in first- and third-person perspective (Ge et al. 2018).

1.2.2.4 Local field potentials' oscillations in the putamen nucleus

In addition to single-cells recordings, the electrophysiology of the BG can be investigated using another neural signal reflecting the dynamic transmission of information through neural networks, the Intracerebral Local Field Potentials (LFPs) (Herreras 2016). LFPs are typically described as the low-frequency component of the electrical potential (usually below 100 or 300 Hz), recorded by a microelectrode in the extracellular space

within a given region of brain tissue (Destexhe and Goldberg, 2015). Besides the easiness of their recordings, the interpretation of the LFPs is challenging, since they reflect an indirect and combined measure of electrical activities in the neighbourhood of the recording electrode (Mitzdorf, 1985; Destexhe and Bédard, 2013). For this reason, action potentials generated by single units have historically received more attention.

However, the importance of the LFPs has been recently remarked: it is now widely accepted that the LFP activity mainly reflects the summation of both excitatory and inhibitory synchronized postsynaptic potentials (Buzsáki et al. 2012; Destexhe and Bédard, 2013 Mazzoni et al., 2015), and therefore provides information about inputs to an area and local processing (Kreiman et al., 2006). Specifically, research focused on LFPs may disclose interaction and integration phenomena not accessible at a single-unit level, and thus increase knowledge on intracortical processing. Furthermore, the combination of LFPs data with single-units and anatomical evidence might bridge the gap between different levels of description of brain functioning (Mitzdorf, 1985).

A substantial body of work in human and nonhuman models revealed that the BG information processing is based on changes in LFPs oscillations in relation to movements, behavioural stimuli, cognitive processing and emotional arousal (Rosa et al., 2015). LFPs oscillations, also known as rhythms, mainly reflect periodic subthreshold membrane potentials fluctuations resulting from the temporal and spatial coordination of the activity of local neuronal populations, but can also be modulated by large-scale network inputs (Frederick et al., 2015). They are typically categorized in five different frequency bands, assumed to subserve distinct physiological roles: delta (1–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (> 30 Hz) bands (Engel and Fries, 2010). Relative short-lasting and localized increases or decreases of oscillatory activity in a specific frequency band in relation to a specific event are defined event-related synchronization (ERS) and event-related desynchronization (ERD), respectively.

The bulk of data on LFPs oscillations in the BG comes from the STN-GPe network (Bevan et al., 2002; Brown et al., 2001; Gatev et al., 2006). However, although very scarce, evidence of oscillations was also found within the striatum, including the putamen nucleus: striatal lower frequency oscillations tend to correlate with resting states, whereas higher frequency oscillatory activity is predominant in alert and behaving animals and

is modulated during behavioural tasks (Courtemanche et al., 2003; Berke et al, 2004; Berke, 2009; Masimore et al., 2004; DeCoteau et al., 2007; Gervasoni et al., 2004).

Beta range oscillations are the best characterized and documented in the BG, since an excessive beta synchronization in this complex is associated with PD motor symptoms, i.e. akinesia and bradykinesia, both in patients and in 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine (MPTP)-treated monkeys (Little et al., 2012; Bergman et al., 1994). Conversely, the administration of dopaminergic medications and deep brain stimulation (DBS), both reducing beta power, improve these parkinsonisms (Levy et al., 2002; Kühn et al., 2006; Müller and Robinson, 2018). However, independently of the parkinsonian condition, brief epochs of beta synchronization in the cortico-basal ganglia networks are physiological and are thought to be involved in motor control (Barone and Rossiter, 2021). Specifically, beta synchronization in the human and nonhuman primates BG, as well as in the sensorimotor cortex, is considered 'antikinetic' because of its transient suppression during dynamic phases of movement (Courtemanche et al., 2003; Sanes and Donoghue, 1993; Cassidy et al. 2002; Kilavik et al., 2013) and its increase in relation to static motor control (i.e. steady contractions or holding) (Baker et al., 1997; Sanes and Donoghue, 1993; Waldert et al., 2015) and following movement cessation (Pfurtscheller et al., 1996b). Concerning the putamen, studying the oscillatory activity in the striatum of healthy awake behaving macaque monkeys during a visually guided saccade task, Courtemanche and colleagues (2003) observed a widespread and synchronous striatal oscillatory activity in the beta-band at rest and during attentive states that did not require active movements. As the monkeys performed saccadic movements during the task, beta rhythm was suppressed at focal recording sites in both the putamen and the caudate nucleus (possibly reflecting functionally-related cortical inputs recipient zones). Sochurkova and Rektor (2003) obtained similar results recording with depth electrodes from the putamen nucleus of a drug-resistant epileptic patient during a self-paced motor task: hand movements of the subject were associated with a power decline in the alpha and beta frequency bands. The same pattern of ERD was observed on the scalp with EEG. An increase of beta power (rebound) also occurred immediately after movement offset. Authors excluded a pathological functioning of the patient's putamen, since no epileptic activity was recorded in that nucleus.

Conversely, movement onset is dynamically and systematically associated with an increase in gamma power in both human and nonhuman primates sensorimotor cortex (Murthy and Fetz, 1992; Salenius et al.,

1996; Bimbi et al., 2018) and BG (Cassidy et al. 2002; Alegre et al., 2005) and in rodents' striatum (DeCoteau et al., 2004; Masimore et al., 2005). Due to their possible role in the promotion of movement, gamma oscillations were defined 'prokinetic' (Brown, 2003). However, in addition to motor control, striatal gamma band synchronization might also be related to motivation and learning processes. Berke and colleagues (2009) observed an increase in the high-gamma (80-100 Hz) power, coherent across the rat motor cortex and dorsal striatum, in relation to reward administration. Similarly, Popescu and colleagues (2009) observed an increase of power in the gamma band across the ventral putamen and amygdala during the presentation of a tone predicting reward delivery: early in the training both unrewarded and rewarded tones elicited a modest increase in gamma power, whereas as learning progressed, gamma power increased selectively in relation to the tone associated with reward.

Theta synchronization within the BG may be related to the selection of a choice during goal-directed behaviours, possibly coordinating the integration of different types of information. Indeed, ERS in the theta band appear to be linked to the evaluation of stimuls-reward associations, retrieval of past and prospective memories and representation of task rules, which require the integration of the incoming sensory stimuli and the appropriate motor response (Womelsdorf et al., 2010). In support of this hypothesis, in a paradigm where rodents learnt to use a tone as an instruction to choose the location of a reward in a T-maze, DeCoteau and colleagues (2007) observed robust and widespread theta-band oscillations in the dorsomedial (associative) and dorsolateral (sensorimotor) putamen immediately after the presentation of the tone and around the start of turning in the correct direction (when a behavioural choice was formed), which decreased after turning. This response was not present in rats that did not learn to use the tone as a cue, or during grooming and resting periods. Tort and colleagues (2008) observed a dynamic cross-frequency coupling between theta and high gamma oscillations within the rat dorsal part of the caudoputamen that peaked during decision making epochs. Authors proposed that this coupling might be associated to the active recall of information relevant for the task performance.

Cortico-striatal alpha oscillations in healthy rats, similarly to beta ones, are suppressed during active movements and predominate during states of immobility or minimal motor activity (Moënne-Loccoz, 2020).

However, rather than reflecting an idling state, striatal alpha might be important for learning and memory consolidation (DeCoteau et al., 2007; Koralek et al., 2010).

Summarizing, putaminal ERDs and ERSs appear to be associated with voluntary movement, reward delivery and decision making. Furthermore, the finding that coherent network oscillations occur within the basal ganglia-thalamocortical circuits supports the idea that the communication between thalamus, cortex and the BG may be facilitated by and possibly founded on this oscillatory activity (Boraud et al., 2005).

1.3 Aim of the study

Data from literature strongly support the idea that the BG, in addition to motor control, also subserves perceptual and cognitive functions. Given this structure's connections with crucial nodes of the MN network (Gerbella et al., 2016) and its modulation during the processing of biological movements (Kesller et al., 2006; Alegre et al., 2010; Ge et al., 2018; Errante and Fogassi, 2020), it is reasonable to assume that the BG might also be involved in social functions, including the processing of others' actions in order to exploit this information for proper social interactions. However, this latter aspect has been poorly investigated.

The aim of the present study is to explore the functional properties of the main input station of the BG, the putamen nucleus, in nonhuman primates during a *mutual action task*, with a specific focus on the representation of one's own and others' actions. In the task, the monkey executes upper limb object-directed actions and observes the same actions performed by an experimenter. The approach used to investigate these properties involved the extracellular recording of both single-units and Local Field Potentials (LFPs) with linear multielectrode probes in the forelimb region of the Putamen of the macaque monkey. Specifically, the present study aimed to investigate the temporal evolution of the LFPs during either the execution or the observation of goal-directed actions, in order to assess the LFP encoding of self and others' actions. The hypothesis is that, through its connections with the MN network, the putamen might exploit at least a partly shared neural substrate to represent own's and others' actions, resulting in a similar LFP modulation in the two conditions. Not yet published data from Bonini's research group (Rotunno et al. FENS 2022) highlight the presence of putaminal single-units modulated during both action execution and observation: the present study represents a complement to these data, assessing how the processing of executed and observed actions occurs

at an intermediate level, i.e. the synaptic integration. We also assessed whether LFPs encoded specific characteristics of observed and executed actions, focusing in particular on the type of grasp.

2 MATERIALS AND METHODS

2.1 Experimental subjects and training procedures

Experiments involved two purpose-bred, pair-housed, adult male *Macaca Mulatta* (Mk1, 12 Kg and Mk2, 9 kg). Training procedure consisted in operant conditioning with positive reinforcement and shaping techniques.

The first training phase consisted in the habituation of the monkeys to the presence and interaction with the researchers, which provided them food from the outside of the cages. Once familiarized with the experimenters, the animals were gradually trained using the same reinforcement technique to sit in a primate chair, which allowed the transport of the monkeys from the animal enclosure to the laboratory, where experiments took place. Afterwards, animals received specialized training for the main experimental task, which will be described in the following section.

The experimental task was subdivided into smaller and easier steps. Once achieved the first step, a second step was chained to the previous one: only when the two chained tasks were completely acquired a further step was added. This procedure has been carried on until the animals were able to perform the whole task. Specific behavioural responses matching or resembling the target behaviour were reinforced using liquid reward (water or fruit juice), whereas undesirable behaviours were gradually extinguished by the absence of positive outcomes. Fresh fruit pieces were also administered to the monkeys at the conclusion of each session, to encourage cooperation and make the training experience as pleasant as possible for the animal. Daily training sessions were held to maintain continuity and to accustom the animals to a predictable routine.

All experimental procedures were conducted in agreement with the European (Directive 2010/63/EU) and Italian (D.lgs 26/2014) legislation for the protection of animals used for scientific purposes, approved by the Veterinarian Animal Care and Use Committee of the University of Parma (Prot. 52/OPBA/2018), and authorized by the Italian Ministry of Health (Aut. Min. 802/2018-PR).

2.2 Behavioural paradigm

Monkeys were trained to perform a *Mutual Action Task* (MAT), which involved a monkey and an experimenter sharing an operational space. The two subjects acted as mutual partners that alternately had to either grasp and hold up a multi-affordance object with a precision grip or a whole hand prehension, or to remain still while observing the partner performing the same actions. Execution and observation trials and grasp types were intermingled in a pseudorandom order.

For the entire duration of the task, the monkey sat in a primate chair at one end of a table, in front of the experimenter sitting on the opposite side. The table was endowed with two manipulanda, located near each agent's hand, and with a multi-affordance device, placed at the centre of the table at a distance of 16 cm from each manipolandum (Fig. 8).

Figure 8 | Experimental setting. The monkey is sitting on one side of the table, in front of the experimenter. In the figure, the experimenter is pressing the manipulandum, while the monkey is reaching the multi-affordance device.

The object, 3D-printed with a polylactic acid (PLA) material, was formed by a cylindrical body (diameter 5.5 cm, height 6 cm) and a parallelepiped (4.5 x 1.5 x 1.5 cm), inserted in the upper end of the cylinder. This conformation allowed two different types of prehension: a *precision grip* (PG), performed with the thumb and the index finger closing on the central parallelepiped, and a *whole hand prehension* (WH), performed with the thumb opposed to the other fingers wrapping around the cylinder. A visual cue specifying the grip type required in each trial appeared on a black rectangular oled screen (2 x 1 cm), located on the upper side of the parallelepiped. An empty square with white borders cued the WH prehension, whereas a full white

square cued the PG. Two metallic plates were applied on the opposite sides of each solid composing the object to obtain, for both grip types, a capacitive circuit sending a TTL signal once closed by the contact with the agent's fingers, indicating the ongoing behavioural event (PG vs WH) (Fig. 9).

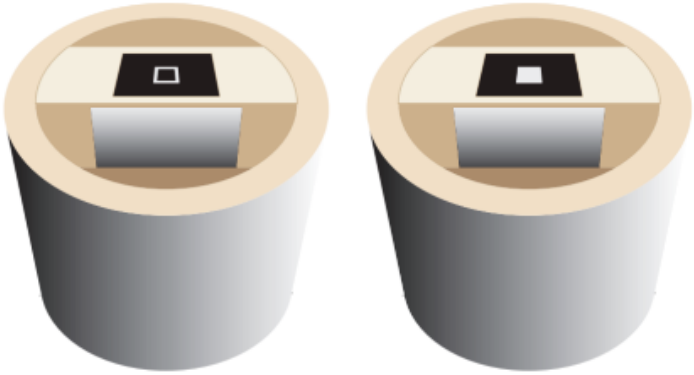


Figure 9 | The multi-affordance object. The figure shows the structure of the object, formed by the cylindrical body and the parallelepiped, endowed with an Oled screen specifying the grip type. On the left, the visual cue (empty square) specifies a WH prehension. On the right, the visual cue (full square) specifies the PG.

An additional auditory cue specified for each trial which of the two agents had to grasp the object. A pure high tone (a sine wave of 1200 Hz) instructed the monkey to perform the grasp (*Go signal*) and the experimenter to remain still, keeping the manipulandum pressed; vice versa, a pure low tone (a sine wave of 300 Hz) instructed the experimenter to grasp and the monkey to remain still (*No-Go signal*).

Each trial started in complete darkness. In the starting position, both subjects seated still and kept pressed the manipulandum with the right hand. After 1 s, either the high or the low sound was presented (*Sound onset*), instructing each subject in an opposite way (*Go cue* vs *No-Go cue*). Then, 770 ms from the sound onset, the oled screen turned on (*Oled onset*), displaying either the empty square, instructing the agent to perform a PG, or the full square, associated with the WH prehension. After 730 ms from the Oled onset, an environmental light turned on, enlightening the object (*Light on*). Subsequently, after further 570 ms, the sound ceased (*Go/No-Go signal*), and during *Go* trials the monkey had to release the manipulandum toreach and grasp the object with the specified prehension type within 1 s (*Grip Condition*), and hold it up for at least 500 ms (*Up-keep*) to receive the reward, administered in a fixed amount through a cannula. Conversely, during *No-Go* trials, the monkey was rewarded only if it remained still pressing the manipolandum throughout the duration of the trial. Next trial began as the agent replaced his hand on the manipulandum. The light stayed on until the completion of the task in half of the trials (*Light Condition*), whereas on the other half it was turned off as the manipulandum was released, so that the agent had to execute the action in the dark (*Dark Condition*). The

Dark Condition ensured that the neural activity recorded from the putamen was effectively related to motor events and did not merely depend on the visual feedback from the monkey's own moving hand (Fig. 10).

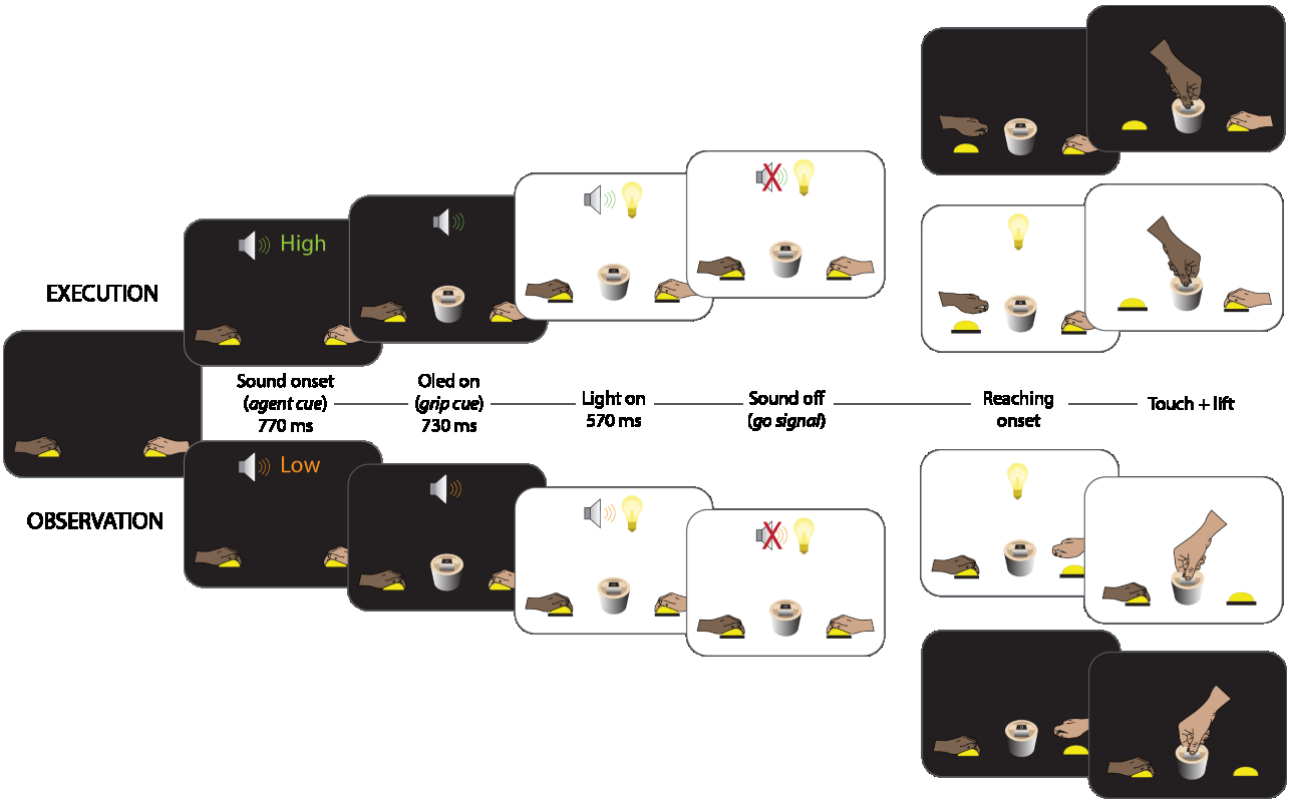


Figure 10 | Temporal sequence of the task.

Each experimental trial was considered correct and analysed if the current agent (the monkey or the experimenter) performed successfully each step and, at the same time, the observer remained still pressing the manipulandum throughout the duration of the trial. Errors led to the abortion of the ongoing trial, which was excluded from subsequent analysis.

To summarize, the task involved 3 dichotomous variables - grip type (*GP* vs *WH*), agent (*EXE* vs *OBS*) and visual feedback (*Light* vs *Dark*) - which combined, resulted in 8 possible experimental conditions (*EXE PG Dark; EXE WH Dark; EXE PG Light; EXE WH Light; OBS PG Dark; OBS WH Dark; OBS PG Light, OBS WH Light*). 15 correct trials were collected for each of the 8 conditions, for a total of 120 correct trials for each recording session.

A further condition (*Barrier Condition*) was added to the task. In this condition, the temporal sequence of events and the behavioural request to the monkey were the same as in any observation trial, but a transparent

plastic barrier was interposed between the monkey and the graspable object, preventing any potential interaction with it.

Each behavioural event was detected by means of distinct contact-sensitive devices that generated a TTL signal at the start and end of hand-target interactions, i.e. object touch (specific for prehension type) and lifting, and at the positioning of the barriers. These signals were sent as inputs to a PC equipped with a dedicated LabView-based software. The software was used to monitor the subjects' performance but also to generate digital output signals associated with the presentation of auditory and visual cues, lighting settings, and reward administration - or withdrawal - in case of errors. All input and output signals were recorded and stored in parallel with the neural data, and subsequently aligned to them for statistical analysis.

2.3 Surgeries and recording devices.

After the completion of the training procedures, both monkeys underwent a surgical procedure for the implantation of a recording chamber to enable subsequent neural acquisitions. However, only one of the monkeys (Mk1) was also implanted with recording probes so far.

Both the chamber and the recording electrodes implants were performed in stereotaxic and aseptic conditions. General anaesthesia was induced by intramuscular injection of ketamine (5 mg/kg) and medetomidine hydrochloride (0.05 mg/kg) and maintained with 2% isofluorane vaporized in 100% oxygen. A multiparametric monitor continuously kept track of the monkey's vital parameters. Saline solution was continuously infused intravenously to keep the animal hydrated, and vitamin A gel was used to guarantee eye hydration during anaesthesia. During and after surgical procedures the animals were given analgesics, broad-spectrum antibiotics, and anti-inflammatory drugs.

2.3.1 Recording chamber

The recording chamber was composed of biocompatible thermoplastic resin, cut and shaped with the 3D Slicer software on a 3D reconstruction of the animal's cranial theca, realized from previously acquired 7T magnetic resonance images. The chamber included a main parallelepipedal body (45 x 50 x 25 mm) and a removable lid that protected a batch of parallel grooves (width 2 mm, inter-groove distance 1 mm), serving as slots for up to 8 connectors blocks (Omnetics Connector Corporation) (Fig. 11). The connectors

interfaced the multielectrode contacts with the headstages, in turn connected to the neural acquisition system (Deuteron Technologies Ltd). During the surgery, the chamber was positioned in accordance with the stereotactic coordinates of the insertion sites and secured to the skull with titanium bone screws and dental cement.

2.3.2 Recording probes

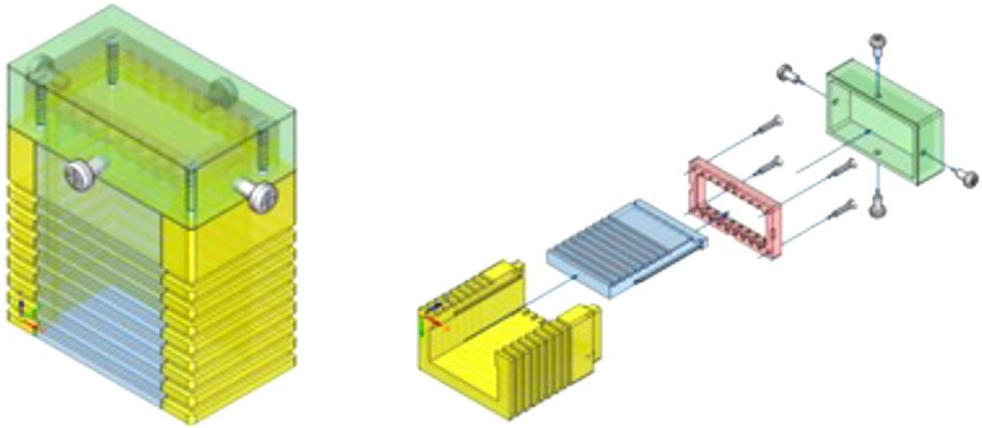


Figure 11 | 3D representation of the recording chamber. On the left, the chamber assembly. On the right, the chamber exploded view. Yellow: main parallelepipedal body. Blue: sliding panel. Pink: constituent with grooves. Green: removable lid.

Once recovered from the surgery for chamber implantation, Mk1 underwent two additional surgeries performed two months away from each other to chronically implant individual linear silicon probes (ATLAS Neuroengineering). A total of five probes were implanted: the first two probes that were implanted during the first surgery were removed and replaced by other three probes during the second surgery.

Each implanted linear silicon probe was composed of a shaft, attached to a highly flexible polyimide-based ribbon cable with a zero-insertion-force (ZIF) connector that could be electrically connected to the recording data logging devices (Fig. 12). Each shaft was 24 mm long, 100 µm thick and 30 µm large, and was endowed with 32 iridium Oxide (IrOx) linearly arranged recording sites with an inter-site distance of 250 µm. All probes were equipped with the pointy tip feature, which significantly reduced any tissue dimpling during probe insertion, thereby facilitating the penetration. The average impedance of the electrodes ranged from 0,23 to 0,29 MΩ.

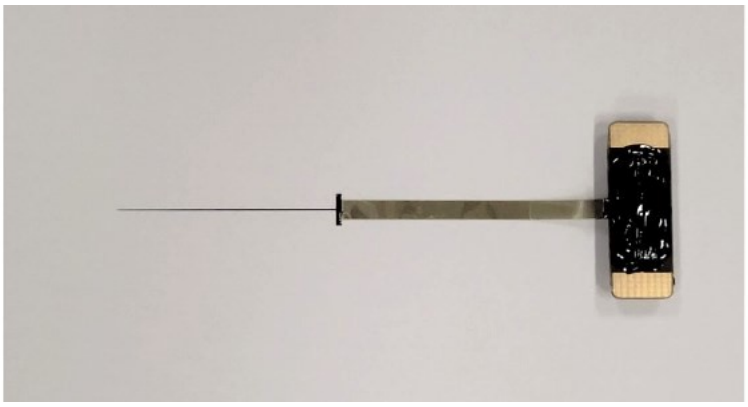


Figure 12 | Linear silicon probe. From the left: recording shaft, ribbon cage, connector.

Insertion sites were determined in terms of stereotaxic coordinates of the region of interest, the left postcommissural putamen (contralateral to the dominant hand used during the experimental task), obtained on the basis of previously acquired MRI images. Penetration angle was set to 90° (vertical), considering the possible deviation in the probe trajectory because of the pointy tip angle. This deviation was calculated using in vitro experiments with agarose that, due to its poro-elastic properties, is a feasible simulation of the brain tissue mechanic features (Pomfret et al., 2013). These tests allowed the detection of a probe deflection of 0.05-0.12 mm per millimetre of probe length, resulting in a total systematic deviation of 1.2-2.9 mm for a 24 mm probe length, always in the opposite direction with respect to the tip's bevelling.

The surgical procedure involved a small craniotomy performed within the recording chamber and the removal of the dura mater, followed by the implantation of probes through an inserter. After the implantation, a collagen-based dural regeneration matrix (DuraGen) was placed around the insertion sites. Finally, liquid dental cement was poured in the recording chamber to replace the removed bone fraction and secure the probes.

A post-mortem examination of the monkey's brain made it possible to assess the exact location of probes' tips. At the end of the study, the animal was deeply anesthetized with an overdose of sodium thiopental and perfused through the left cardiac ventricle consecutively with saline (about 2 L in 10 min), 3.5% formaldehyde (5 L in 30 min), and 5% glycerol (3 L in 20 min), all prepared in 0.1 M phosphate buffer, pH 7.4. The brain was then blocked coronally on a stereotaxic apparatus, removed from the skull,

and placed in 10% buffered glycerol for 3 days and 20% buffered glycerol for 4 days. Finally, it was cut frozen into coronal sections of 60 µm thickness, and two series of them were stained with the Nissl method (0.1% thionin in 0.1 M acetate buffer, pH 3.7).

2.4 Neural data acquisition

Neural signals were recorded using a small, lightweight neural logger (Deuteron Technologies Ltd) that allowed the acquisition of neural data from the monkey in head-free conditions. Indeed, although the monkey's movement was limited by the primate chair during the task, the head was unrestrained and all upper body movements were allowed. Specifically, for the first implant (64 channels) a RatLog64 was used (Fig. 13), whereas a RatLog128 was employed for the second implant (96 channel). The device was powered by a small external battery (two hours maximum duration) to which it was connected via a short cable, and it was equipped with a magnetic on/off switch to ensure the possibility of prompt response in the event of system crash or malfunctioning during a recording session.

Once the logger device was linked to the electrode arrays, all the components were sealed with a cover on top of the recording chamber. A digital bandpass filter with upper and lower cut-off frequencies set at 2 and 7000 Hz, respectively, and a conversion rate of 32000 Hz was applied on each channel, permitting to sample both local field potentials (LFPs) and single/multi-unit activity. Signals were amplified, digitized, and locally stored in a MicroSD memory card (64 GB) to prevent possible transmission errors. The logger communicated with a computer through a transceiver with 4 BNC connectors for digital inputs and one for digital outputs, which was connected to the host computer via USB.

Figure 13 | Deuteron neural logger (RatLog64). RatLog-64 with two stacked headstages

2.5 Neural data analysis

Analyses concerning the monkey's execution trials were performed considering the Dark Condition only (*EXE PG Dark; EXE WH Dark*) to exclude the possibility that the recorded neural activity during the execution of the action could be related to visual feedback of the monkey's own grasping actions. Conversely, neuronal responses during the monkey's observation trials were analysed considering only the Light Condition (*OBS PG Light; OBS WH Light*).

All data pre-processing and spectrograms were performed using Python 3. In order to obtain LFPs activity, raw data were further bandpass-filtered (2-300 Hz) with a fourth order low pass digital filter (Butterworth), applying the function *signal.butter* from the package *scipy*. Then, the recorded signal was subsampled at 3200 Hz and cut into trials aligned to the event *Sound Off (*which instructed the agent to release the manipulandum, reach and grasp the object with the specified prehension), extracting the part of the signal between 4.3 s before and 4.0 s after that event.

To estimate the temporal structure in the LFP, we computed the one-dimensional Discrete Fourier Transform (DFT) on the time series signal by means of an efficient Fast Fourier Transform (FFT) algorithm, using the function *ff.rfft* from the package *numpy*. We set a time window of 0.5 s, a step size of 0.3125 ms and a 0.8 percentage overlap.

We thus obtained spectrograms S(f,t) for each frequency (f) and time (t). A proper smoothing filter through a cubic spline interpolation was then applied to the 2D grid of the spectrogram. First, spectrograms were computed for each recording session and experimental condition (*EXE PG Dark; EXE WH Dark, OBS PG Light; OBS WH Light*), averaging across recording channels (irrespectively of the electrode depth), probes and trials within the same condition (see Results). We considered for our analysis only signal recorded from channels in which single units were detected, to exclude the possibility to analyse signals sampled from non-recording/broken electrodes. Next, separately for each experimental condition, a grand-averaged spectrogram was obtained by averaging all recording sessions and implants.

To better appreciate modulations produced by experimental conditions we computed normalized spectrograms dividing, for each frequency, LFP activity by its baseline value on a trial-by trial basis (see Waldert et al., 2015). Specifically, for each trial, the amplitude modulation in each frequency bin was divided

by the frequency bin specific average amplitude at baseline B(f). Baseline was defined, for both EXE and OBS trials, as the time interval of 500 ms preceding the cue-sound presentation (*Sound On)*, during which both the experimenter and the monkey remained in the dark, keeping the manipulandum pressed. The obtained renormalized spectrograms were expressed in decibel (dB): $S_{norm}(f,t) = 10 \cdot \log_{10} S/B$.

Based on previous literature on the BG (see Courtemanche et al., 2003; Sochurkova and Rektor, 2003; Berke et al., 2004; Berke et al., 2009) and motor cortex (see Caggiano et al., 2014; Waldert et al., 2015) and the obtained spectrograms, we considered for our subsequent analyses four frequency bands: a low-frequency band (2 – 8 Hz), including delta and theta frequencies; a low-medium frequency band (9 – 25 Hz), including high alpha and low beta frequencies; a medium-high frequency band (26 – 40 Hz), including high beta and low gamma frequencies; a high frequency band (60 – 100 Hz) including high-gamma frequencies. To assess the statistical significance of the LFP power modulations produced by action execution and observation and grip type, we conducted a 2 x 6 repeated measures ANOVA, separately for action execution and action observation conditions and for each of the considered frequency bands, performed with R studio (*anova_test* function, from the package *rstatix*). The two independent variables were grip (*WH* vs *PG*) and epoch (*Baseline, Sound On, Oled On, Light On, Sound Off, Motor*); the dependent variable was the LFP power. First, on a trial-by-trial basis and separately for each agent and frequency band, we esteemed the mean LFP power, averaged across recording channels and probes, during the 6 epochs that included:

- *Baseline*: the 500 ms time interval preceding the Sound On event
- *Sound On*: the 770 ms time interval following the presentation of either the high (EXE) or the low sound (OBS), cueing the agent of the current trial
- *Oled On*: the 730 ms time interval following the lighting of the oled screen, specifying the grip type
- *Light on*: the 570 ms time interval during which the light turned on to show the target object
- *Sound Off*: the time interval following the offset of the sound (the go signal that instructed either the experimenter or the monkey to reach and grasp the target object) and preceding the release of the manipulandum. For each experimental condition, we used the median time interval between these two events, calculated over all sessions of the two implants (*EXE PG Dark*: 281 ms; *EXE WH Dark*: 278 ms; *OBS PG Light*: 368 ms; *OBS WH Light*: 380 ms).

- *Motor*: the 750 ms time interval following the monkey's or the experimenter's release of the manipulandum and preceding the reward administration.

All the analysis were carried out by averaging the LFP power over the 15 correct trials of each experimental condition within the same recording session, and using a single value for each condition and session (n = 19) as an entry data for the ANOVA. In addition to the statistical significance, we evaluated the effect size in order to assess the relevance of our results. The factorial ANOVA was followed by post hoc pairwise t-tests, using Bonferroni correction for the familywise error-rate (*pairwise.t.test* function, from the package *RDocumentation*). To assess the statistical significance of the differences in the LFP power modulation between the action execution and action observation conditions, we also conducted a priori contrasts between the two conditions within each level of the variable epoch (*contrast* function, from the package *emmeans*).

3 RESULTS

In the present study, we analysed LFPs collected during 19 recording sessions (6 sessions for the first implant and 13 for the second implant). Specifically, we investigated the temporal evolution of the LFP power during the execution and observation of grasping actions, with a specific focus on the encoding of the acting agent and the grip type. The post-mortem Nissl staining confirmed the correct location of the probes in the putamen nucleus (Fig. 14).

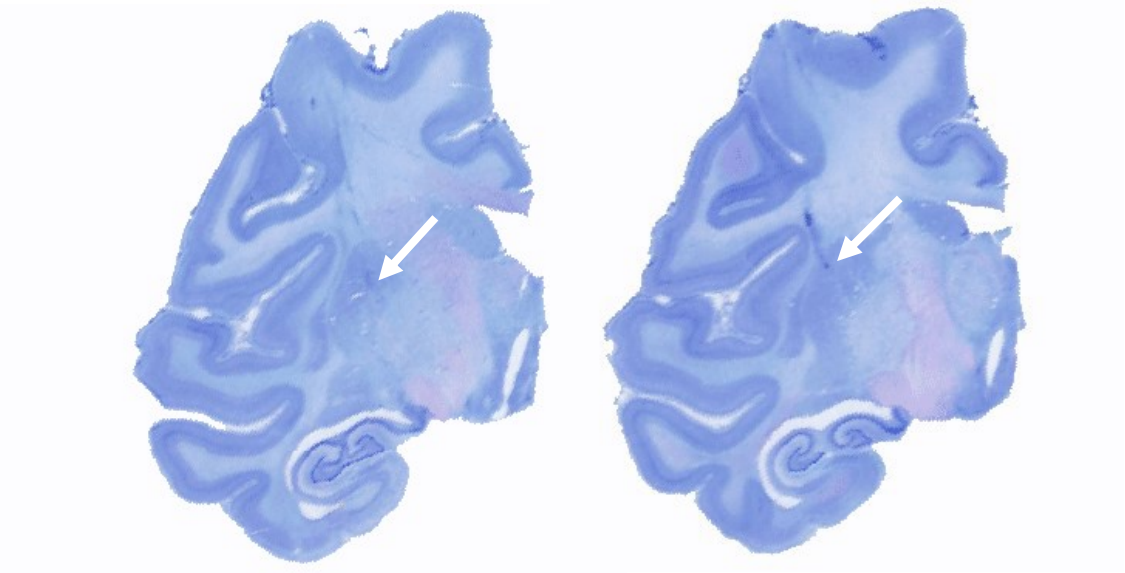


Figure 14 | Nissl-stained coronal sections of Mk1's brain. Stains in dark blue indicated by white arrows represent the location of the electrodes' tips.

The recorded LFP power in different recording channels within the same probe as well as between different probes did not reveal relevant differences, neither between depths nor between implant coordinates. Figure 15 shows LFPs recorded during a session from the second implant, comparing channels at three different depths (rows) in each of the three recording probes (350, 355 and 352, in columns). It is evident the remarkable similarity of LFP modulation in the various frequency bands across different depths. These findings highlight the substantial homogeneity of LFP modulation in the putamen during the same type of trials, in line with previous findings (Courtemanche et al., 2003), and induced us to average the contribution of different electrodes of the same probe for further analyses.

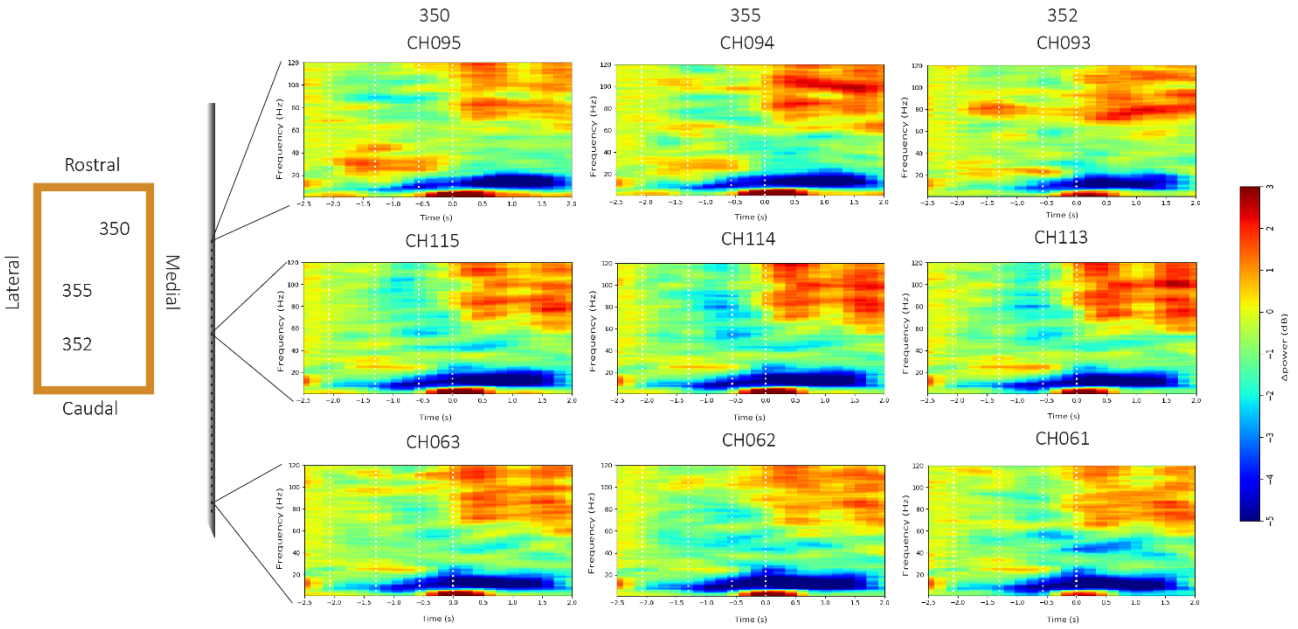


Figure 15 | **LFPs across recording probes and depths (second implant)**. On the left, a schematic representation of the coordinates of the three electrodes within the recording chamber (represented in orange). On the right, spectrograms obtained by averaging 15 correct trials of the experimental condition *EXE PG Dark*, collected over a session of the second implant. Each column specifies the recording probe (350, 352, 355), whereas each row indicates a specific recording depth: from the top, a superficial channel (CH95, CH94, CH93), an intermediate channel (CH115, CH114, CH113) and a deep channel (CH63, CH62, CH61). White dashed lines represent, from the left, the following events: Sound On, Oled On, Light On, Sound Off (t = 0).

The similarity in the average LFP modulation between the first (Fig. 16A) and second (Fig. 16B) implant prompted us to average the LFP signals also across implants for representative purposes (Fig. 16C). In brief, within each of the two implants we found a clear desynchronization of the alpha/beta band, and a synchronization of both delta/theta and high gamma bands, comparable within each of the considered experimental conditions. Specifically, for both implants, in the EXE conditions (including both PG and WH grips) the alpha/beta suppression was earlier and longer compared to OBS conditions, starting approximately from the visual presentation of the target object and lasting throughout the entire duration of the executed action. On the other hand, in OBS conditions this desynchronization was overall less marked and mostly concentrated during the experimenter's actual grasp execution for both PG and WH grip, although a slight suppression was still appreciable at a visual inspection after the presentation of the target object: this trend was extremely reproducible across the two implants. Similarly, both the gamma and the delta/theta band synchronization were very similar within each experimental condition across the two implants: both action execution and observation were associated with a power increase in these two frequency bands, albeit less intense during action observation. Action observation was also characterized by an increase in the low gamma band, modulation that was not present during action execution. The only noticeable difference between the

two implants concerned the modulation of the high beta/low gamma frequency band within the action execution conditions (both PG and WH grips), which was slightly more evident in the first implant, although also present in the second implant.

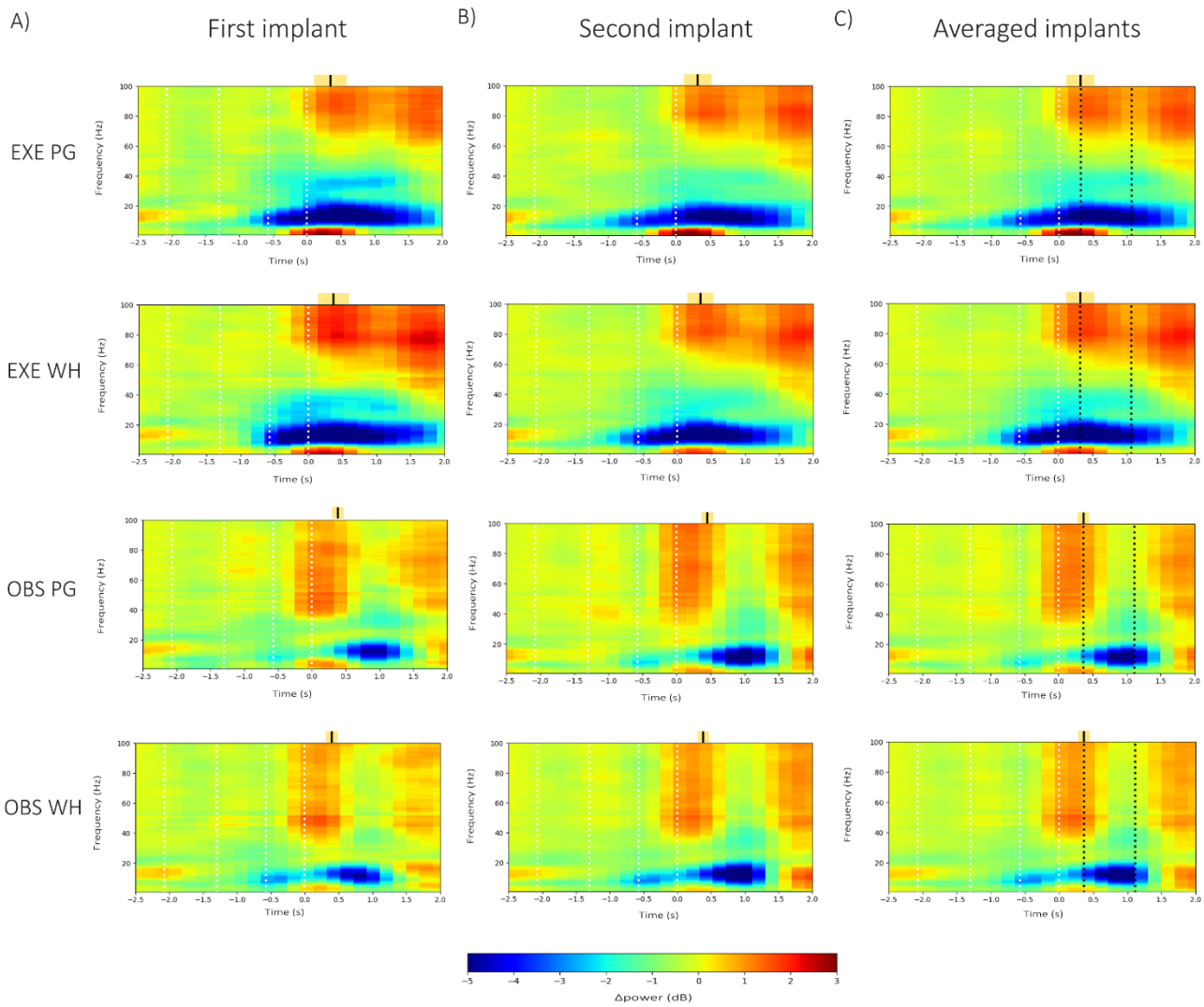


Figure 16 | **LFPs across implants**. A) Spectrograms obtained by averaging all recording sessions, probes and channels (only those in which single units were detected) within the first implant, separately for each experimental condition (rows). B) Analogue spectrograms, obtained for the second implant. C) The final spectrogram, obtained by the combination of the two implants. From the left, white dashed lines represent *Sound On*, *Oled On*, *Light On* and *Sound Off* (t = 0). Black solid lines surrounded by yellow marks represent median ± SD of the difference between the *Sound Off* event (the cue instructing the agent to reach and grasp the target object) and the effective release of the manipulandum by either the monkey (EXE) or the experimenter (OBS). Black dashed lines represent the motor epoch considered for following analyses.

3.1 LFP encoding of action execution and observation

To better capture the main possible differences in LFP modulation associated with action execution and observation, we first computed the LFP spectrogram by averaging the modulation associated to different grip types (Fig. 17). It is clear that the main differences concern a stronger suppression of the alpha/beta band power and a greater enhancement of the high gamma and delta/theta band power in execution relative to observation condition. Interestingly, these modulations, especially those in the lower frequency bands, appear to occur earlier during action execution than observation.

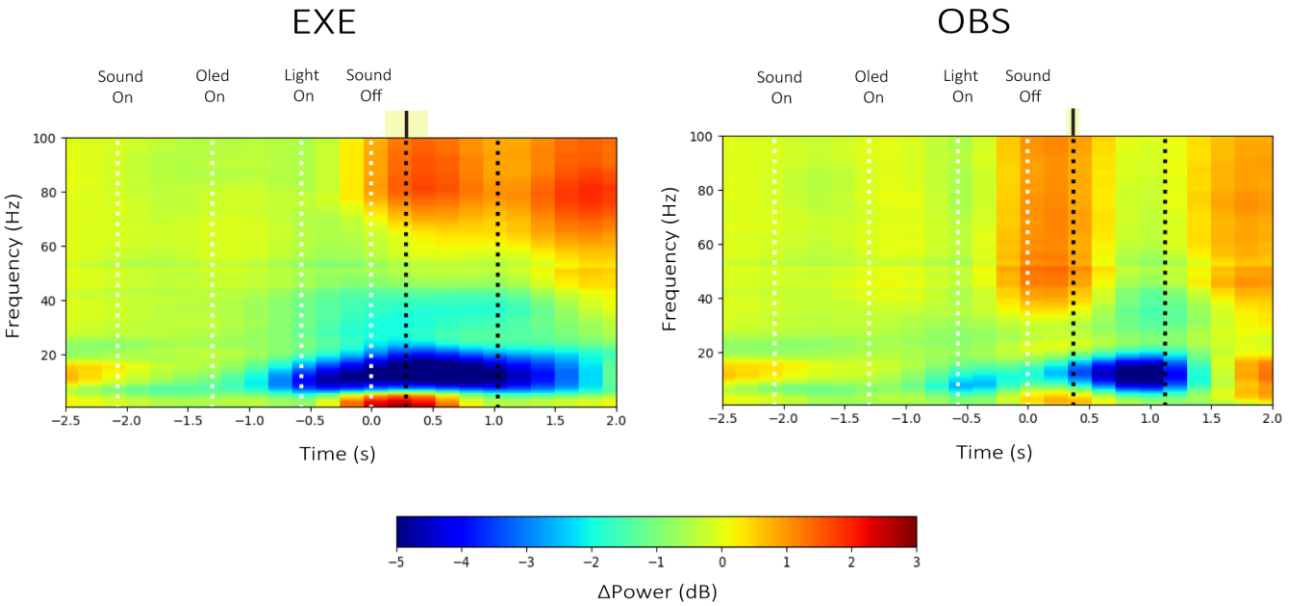


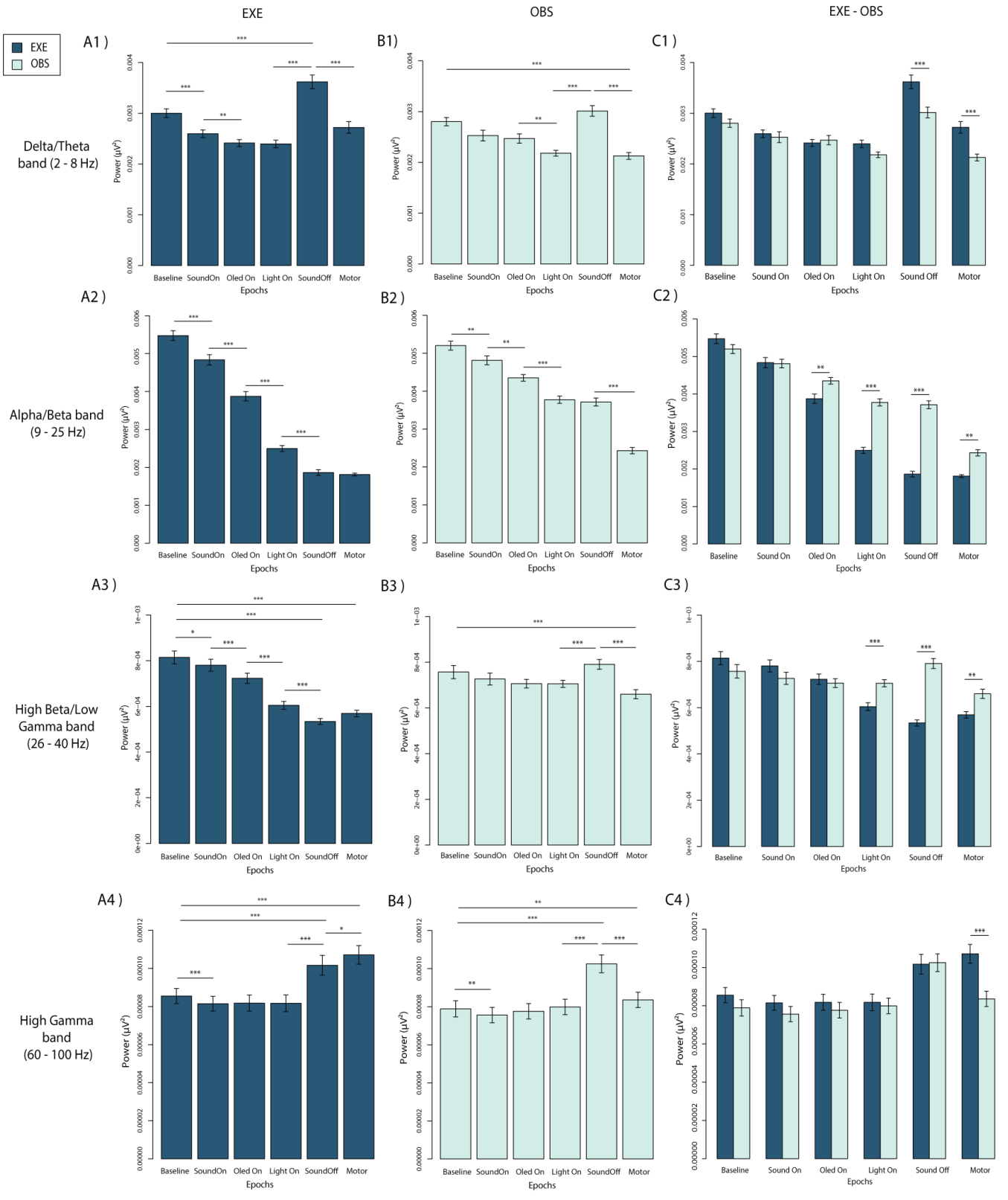
Figure 17 | **LFPs during action execution and observation, irrespectively of the grip type**. From the left, white dashed lines represent *Sound On*, *Oled On*, *Light On* and *Sound Off* events (t = 0). Black solid lines surrounded by yellow marks represent median ± MAD of the difference between the *Sound Off* event (the cue instructing the agent to reach and grasp the target object) and the effective release of the manipulandum by either the monkey (EXE) or the experimenter (OBS). Black dashed lines delimit the motor epoch.

Analysing in detail the LFP power modulation in each of the considered frequency bands, separately for the action execution and action observation conditions, we found for all of them a significant main effect of epoch: each frequency band exhibited a significant modulation across epochs, irrespectively of the grip type (for details, see Fig. 18A5 for EXE and Fig. 18B5). Specifically, for both EXE and OBS conditions, LFP power in the low frequency band showed slight decrease after the baseline epoch, followed by a sharp and brief synchronization after the go cue, no longer present during the motor epoch (for significant comparisons, see Fig. 18A1 for EXE and Fig. 18B1 for OBS). Concerning the low-medium and the medium-high frequency bands, they both followed the same progressive suppression trend, which peaked during the motor epoch (for significant comparisons, see Fig. 18A2 and 18A3 for EXE and Fig. 18B2 and 18B3 for OBS). Finally, the LFP

power in the high frequency band was characterized by a clear enhancement after the go cue that lasted throughout the effective motor epoch for the EXE condition (for significant comparisons, see Fig. 18A4), whereas in the OBS condition this increase was mostly concentrated after the go cue (for significant comparisons, see Fig. 18B4).

Then, we assessed the presence of significant differences in the LFP power modulation between the EXE and OBS conditions within each epoch. The low frequency band was characterized by a significantly higher LFP power during EXE compared to OBS condition, both after the go cue and during the effective grasp ($p < 0.001$ for comparisons within both the *Sound Off* and *Motor* epochs; see Fig. 18C1). With respect to the medium-low frequency band, this different modulation was characterized by a more marked suppression for EXE compared to OBS condition starting from the oled onset, specifying the correct grip, and lasting through the visual presentation of the object, the go cue and the grasp ($p < 0.001$ for each comparison within *Light On* and *Sound Off* and $p < 0.01$ for each comparison within the *Oled On* and *Motor* epochs; see Fig. 18C2). The different LFP modulation for EXE and OBS in the medium-high frequency band was concentrated after the visual presentation of the object, the go cue and the effective grasp ($p < 0.01$ for comparisons within the *Light On* and the *Motor* epochs, $p < 0.001$ for the comparison within the *Sound Off* epoch; see Fig. 18C3). Finally, the high frequency band was differently modulated only during the effective grasp, with a more increased power in EXE compared to OBS condition ($p < 0.001$ for the comparison within the *Motor* epoch, see Fig. 18C4).

Summarizing, some differences in the encoding of one's own and others' actions were reflected by all the considered frequency bands. These different LFP modulations were characterized by either a more marked synchronization - for the low and high frequency bands - or desynchronization - for the low-medium and the medium-high frequency bands - during action execution compared to action observation, which, overall, was associated with less intense modulations in both directions.



A5) EXE

Freq. band	Main effect of epoch
Delta/Theta (2 - 8 Hz)	p < 0.001. F = 28.60
Alpha/Beta (9 - 25 Hz)	p < 0.001. F = 233.90
High Beta/ Low Gamma (26- 40 Hz)	p < 0.001. F = 91.82
High Gamma (60 - 100 Hz)	p < 0.001. F = 91.71

B5) OBS

Freq. band	Main effect of epoch
Delta/Theta (2 - 8 Hz)	p < 0.001. F = 18.55
Alpha/Beta (9 - 25 Hz)	p < 0.001. F = 119.90
High Beta/ Low Gamma (26- 40 Hz)	p < 0.001. F = 12.88
High Gamma (60 - 100 Hz)	p < 0.001. F = 81.10

C5) EXE vs OBS

Freq. band	Baseline	S. On	O. On	L. On	S. Off	Motor
Delta/Theta (2 - 8 Hz)	ns	ns	ns	ns	p < 0.001	p < 0.001
Alpha/Beta (9 - 25 Hz)	ns	ns	p < 0.01	p < 0.001	p < 0.001	p < 0.01
High Beta/ Low Gamma (26- 40 Hz)	ns	ns	ns	p < 0.001	p < 0.001	p < 0.01
High Gamma (60 - 100 Hz)	ns	ns	ns	ns	ns	p < 0.001

Figure 18 | **LFP modulation in each of the considered frequency bands.** A1-4) Barplots representing the mean LFP power (± SE) for each level of the epoch variable in the EXE condition, collapsed across grip type. The figure highlights only significant differences between each epoch and the following one, and those between the motor/pre-motor (*Sound Off*) epochs and baseline. B1-4) Same barplots, but for the OBS condition. C1-4) The same data are represented by comparing EXE and OBS and highlighting significant differences between the two conditions within the same epoch. *p < 0.05; **p < 0.01; ***p < 0.001. A5, B5) p values and respective F statistics associated with main effect of epoch, for the EXE and OBS condition, respectively. C) Statistical significance of the a priori contrasts between EXE and OBS within each level of the variable epoch.

3.2 LFP modulation in relation to the reaction time

Next, we tried to assess whether modulations in the LFP power during action execution could be related to motor rather than sensory and/or cognitive aspects. In this regard, we identified (by taking into consideration all sessions and implants) the 30 correct trials in which the time interval between the cue that instructed the monkey to reach and grasp the target object and the effective release of the manipulandum was maximum, and the 30 trials where this interval was minimum, to assess the possible presence of differences in the LFP modulation in relation to the reaction time (Fig. 19).

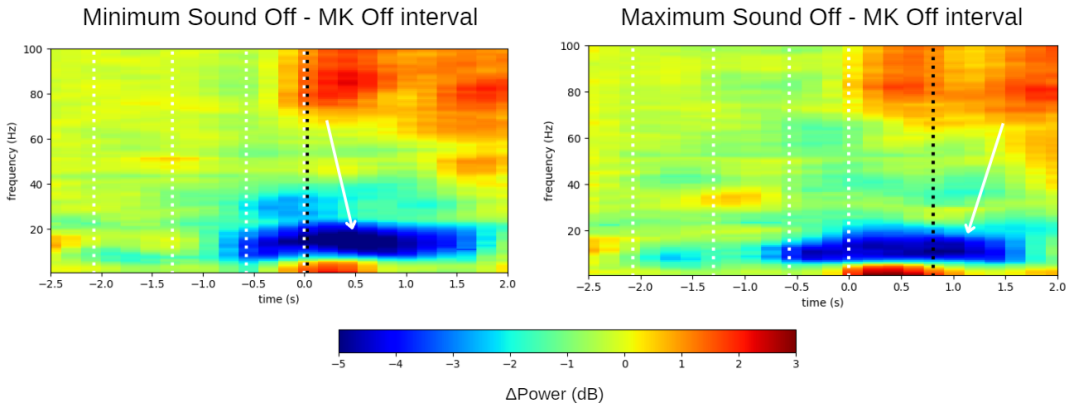


Figure 19 | **LFP modulation in relation to the reaction time.** On the left, the 30 trials (15 PG and 15 WH) in which the reaction time was minimum, while on the right the 30 trials (15 PG and 15 WH) in which the reaction time was maximum. White dashed lines represent, from the left: Sound On, Oled On, Light On, Sound Off (t = 0). Black dashed lines represent the mean reaction time for each group of trials, i.e. the difference between the go cue (*Sound Off*) and the release of the manipulandum (*MK Off*). Min reaction time = 0.0276 ± 0.011 SD, Max reaction time = 0.8066 ± 0.051 SD). White arrows indicate the point of maximum suppression of the medium-low frequency band.

No clear differences were observed for the low frequency band (2 – 8 Hz) across the two groups of trials: the synchronization occurred immediately after the go cue, regardless of whether the action already started or not. Similarly, the suppression of the low-medium frequency band (9 – 25 Hz) started approximately 500 ms before the go cue in both groups, apparently triggered by the environmental light onset, lasting longer for trials with longer reaction times: the maximal desynchronization (represented in dark blue) was observed in both cases immediately after the release of the manipulandum, suggesting that, at least in part, it may be related to preparatory and motor aspects. When the reaction time was minimum, we also observed a

suppression of the medium-high frequency (26 – 40 Hz) immediately before action execution that, however, was not present when the reaction time was maximal. Regarding the high frequency band (60 – 100 Hz), the synchronization tended to start earlier the faster the reaction time (approximately 250 ms before the *Sound Off* vs immediately after the *Sound Off*); nonetheless, it appears to be linked to the Go signal, thus suggesting it may indexes a preparatory rather than overtly motor process..

3.3 LFP encoding of grip type during EXE and OBS

Finally, we wanted to assess whether LFPs could encode different aspects of action, focusing in particular on the grip type. We thus investigated the two-way interaction effect of grip and epoch, separately for EXE and OBS conditions, for each of the considered frequency bands. Figure 20 compares LFPs during EXE and OBS conditions, separately for grip type.

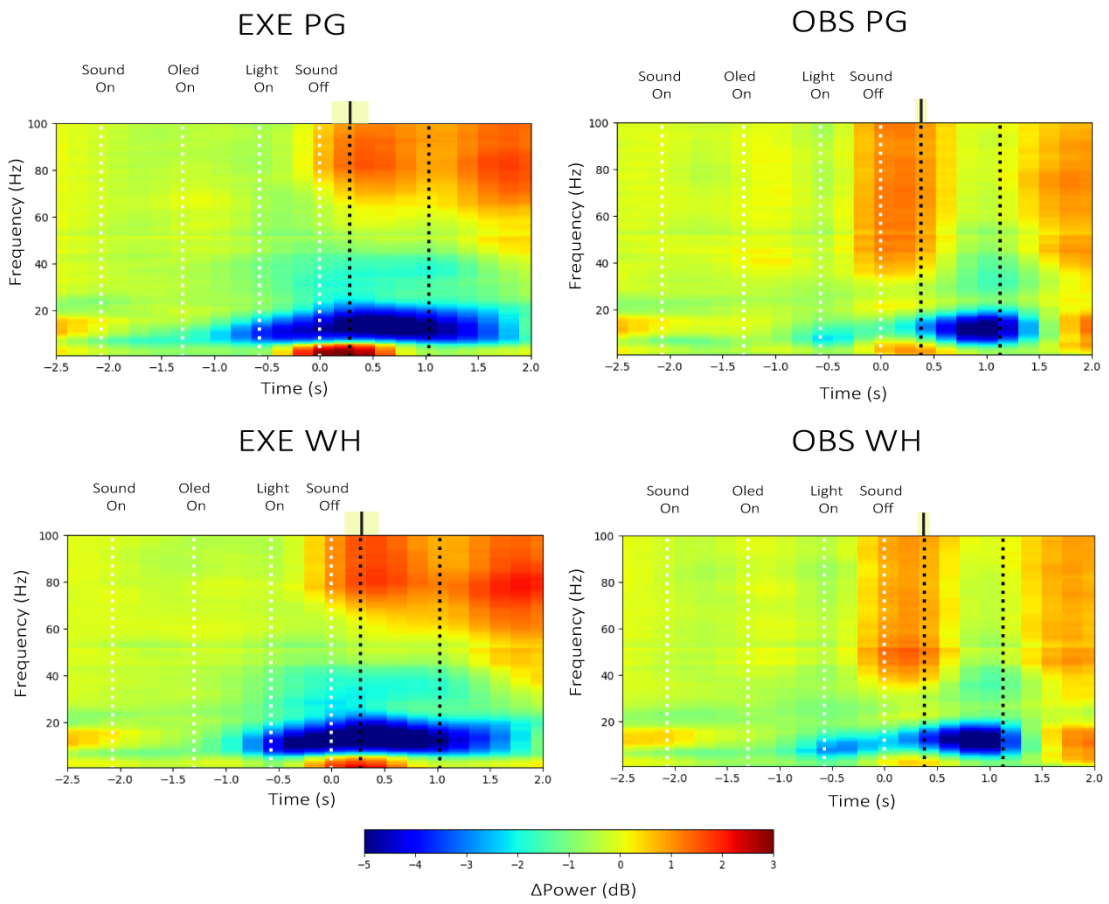


Figure 20 | **LFPs during action execution and observation, separately for the grip type**. From the left, white dashed lines represent *Sound On*, *Oled On*, *Light On* and *Sound Off* (t = 0). Black solid lines surrounded by yellow marks represent median (± MAD) of the difference between the *Sound Off* event and the effective release of the manipulandum by either the monkey (EXE) or the experimenter (OBS). Black dashed lines delimit the motor epoch.

A significant two-way interaction of grip and epoch was observed for the low-frequency band in the EXE condition ($p < 0.001$, $F = 17.83$). We thus investigated the effect of grip on the LFP power at the level of each epoch (see Fig. 21A). We found that PG grip was associated with a significantly higher LFP power, compared to WH, after both the visual presentation of the target object and the go cue ($p < 0.01$ for the within the *Light On* epoch; $p < 0.001$, for the comparison within the *Sound Off* epoch; see Fig. 21E for significant comparisons), but not during the effective grasp. On the other hand, no significant two-way interaction effects were found for the other three frequency bands (see Fig. 21B, 21C, 21D).

Summarizing, the low frequency band is the only band that appears to discriminate between the two different grip types, with PG grip associated with a higher LFP power compared to WH during action execution.

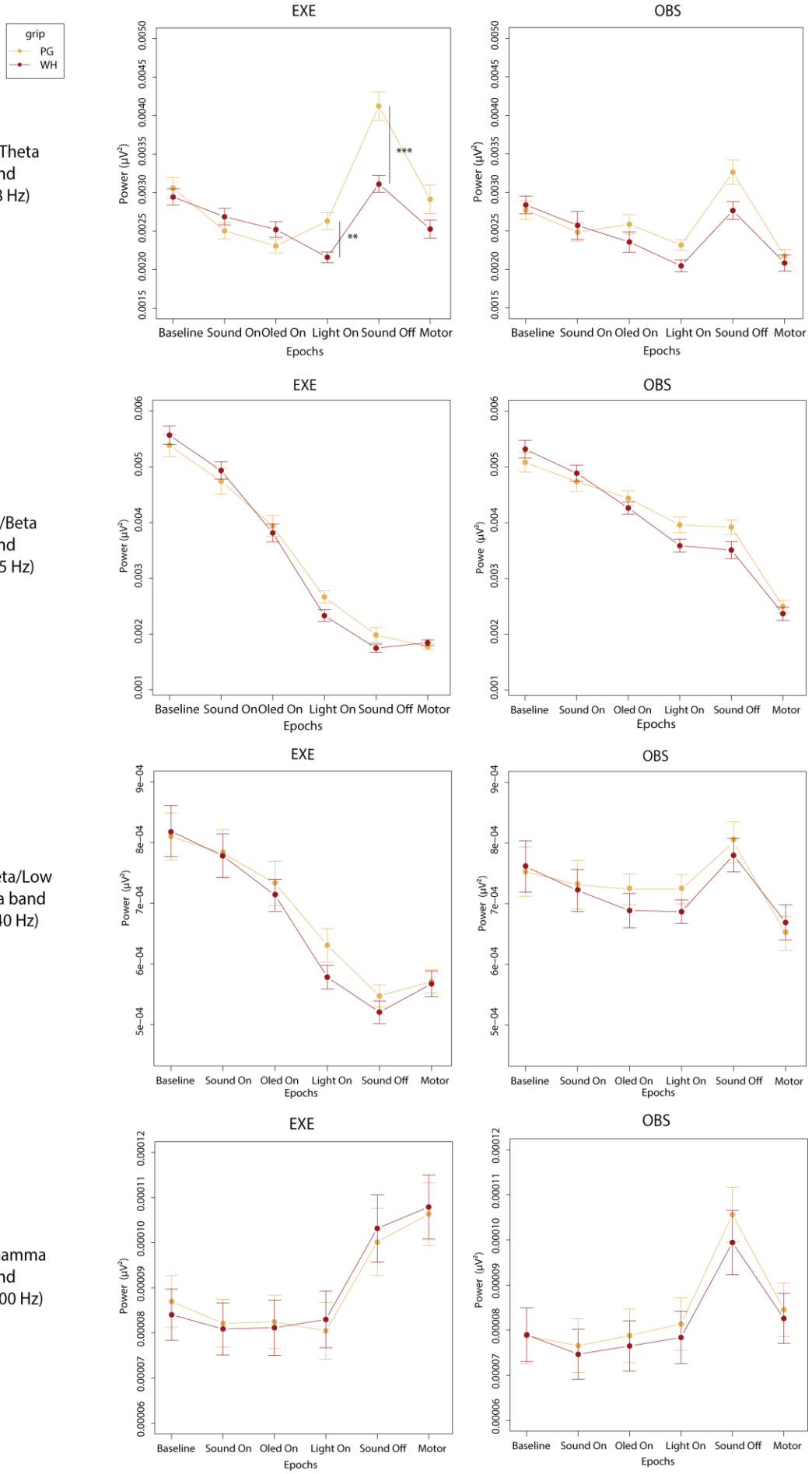

grip
PG
WH
Delta/Theta band (2 - 8 Hz)
Alpha/Beta band (9 - 25 Hz)
High Beta/Low Gamma band (26 - 40 Hz)
High Gamma band (60 - 100 Hz)
EXE
OBS
Power (μV²)
Epochs
Baseline
Sound On
Oled On
Light On
Sound Off
Motor
***
**

Figure 21 | **LFPs during action execution and observation, separately for the grip type in each of the considered frequency bands**. A, B, C, D) The graphs represents the mean LFP power (± SE) during the six time epochs, separately for agent (EXE on the left and OBS on the right) and grip type. Asterisks highlight significant post hoc comparisons in the low frequency band. *p < 0.05; **p < 0.01; ***p < 0.001

4 DISCUSSION

The mirror neuron (MN) network is a complex system composed of several reciprocally interconnected cortical areas that play a key role in matching the visual description of an observed motor action with a motor representation in the observer's repertoire (Fogassi and Ferrari, 2011). According to the social affordance hypothesis (Orban et al., 2021), this network could play a role in planning and preparing social interactions. Recent anatomical data suggest that also subcortical areas, including the BG, might contribute to the MN network. Indeed, the putamen nucleus - the main input station of the BG - receives dense projections from cortical areas forming the lateral grasping network (Gerbella et al., 2016). Notably, these areas also represent crucial nodes of the hand MN network. Although the motor role of the putamen is widely accepted (see DeLong, 1973; DeLong and Strick, 1974; Crutcher and DeLong, 1984; Kimura, 1990), its specific involvement in planning and execution of grasping actions, as well as in motor-based high-order perceptual and social functions, including the encoding others' observed actions, is still poorly understood.

The present study, therefore, aimed at investigating the functional proprieties of the macaque putamen nucleus during a Mutual Action Task in which the monkey and the experimenter alternately had to either grasp and hold up a multi-affordance object with a precision grip or a whole hand prehension, or to remain still while observing the partner performing the same actions. This task allowed us not only to assess the putamen encoding of one's own and others' action, but also the encoding of specific aspects of actions, focusing on particular on the grip type. The approach used to investigate these properties involved the extracellular recording of Local Field Potentials (LFPs), a signal that mainly reflects postsynaptic potentials (Buzsáki et al. 2012) and that therefore provides information about inputs to an area and its local processing (Kreiman et al., 2006).

4.1 LFP encoding of one's own and others' observed action

We found that both action execution and action observation were associated with a desynchronization of the alpha/beta and high-beta/low-gamma bands, and with a synchronization of the delta/theta and high gamma bands. Although overall less marked during action observation compared to action execution, these modulations had similar characteristics and followed the same pattern across trials' epochs in the two conditions.

We observed, for both action execution and observation conditions, a sharp ERS of the low frequency band (2 – 8 Hz) during the pre-movement epoch that decreased during either the experimenter's or monkey's effective grasp, Notably, this modulation did not seem to be affected by the reaction time; instead, it tended to concentrate immediately after the go cue, suggesting that it may not primarily reflect motor-related activity, but rather it could be involved in decision-making aspects. This is in accordance with previous findings suggesting that a synchronization of the theta band across limbic, striatal and cortical nodes may be related to the selection of a choice during goal-directed behaviours (Womelsdorf et al., 2010). Indeed, investigating LFP in the rodent putamen (including both the dorsomedial and the dorsolateral sectors), DeCoteau observed a widespread synchronization of this band immediately after the presentation of a tone instructing the animal the correct direction in a maze to receive a reward. Tort et al. (2008) observed a similar enhancement of the theta band LFP power during decision-making epochs in the rat caudal putamen. We can reasonably rule out the hypothesis that this synchronization may be associated with purely perceptual aspects, since in our case the go cue coincided with the turning off of the sound, whereas in DeCoteau's study the cue coincided with its presentation. Otherwise, if the response was due to hearing the sound, we would have observed a synchronization throughout sensory epochs of the task. With respect to the delta frequency band, coherent delta band oscillations across monkey's frontal and parietal cortical areas appear, as well as theta band oscillations, to correlate with decision making and to be modulated by different decision alternatives (Nácher et al., 2013). To date, no study has investigated the functional responses of the putamen during action observation. However, it is reasonable to assume that the delta/theta synchronization in the observation condition could reflect the active choice to inhibit the impending motor response. In light of the well-known role of the putamen in motor-selection processes based on the current context (Yin and Knowlton, 2006), these results suggest that the theta frequency band synchronization in this nucleus might be associated with the active recalling of information relevant for the task and the selection of the proper response, also in agreement with findings suggesting that oscillations at lower frequencies could play a key role in long-range integrative processes (Von Stein and Sarnthein, 2000; Nácher et al., 2013).

Concerning the alpha/beta band, in accordance with our results showing a marked suppression during both action execution and observation, Alegre and colleagues (2010) described a beta (15 – 30 Hz) ERD during both action execution and observation of self-initiated wrist extensions movements in the STN of PD patients

on anti-parkinsonian medications. Similarly to what we observed, this modulation was less intense during action observation compared to action execution. Authors also found that action execution, but not observation, was characterized by an ERD of the alpha band (8 – 12 Hz). This latter result is only partially in agreement with our results, as we observed a desynchronization of this band also during action observation. However, supporting our results, Marceglia et al. (2009) described a suppression in the high-alpha/low-beta (10 -18 Hz) band in the STN of PD patients during the observation of a movie clip showing grasping actions. In Alegre's study (2010) the ERD of the alpha/beta band in the execution condition started approximately 1 s before movement onset, reached a minimum value during the effective movement, and lasted until the end of the action (similar findings were found by a previous study of the same authors: Alegre et al., 2005). On the other hand, during action observation, beta ERD started approximately 100 ms before movement onset and, as well as for action execution trials, peaked during the effective movement and lasted for the entire movement duration. These findings fit well with our results; indeed, although in our case a significant alpha/beta band ERD in the execution condition was already observed in the epoch after the baseline, i.e. after agent and grip specification, this suppression was especially marked after the visual presentation of the object, namely approximately 1 s before the actual movement onset, and was prolonged throughout the entire duration of the grasping. It is possible that we found an earlier significant decrease in power since both agent and grip specification were information relevant for planning the impending action. In further support of the relationship between the suppression of the alpha/beta band and motor activity, we observed that the peak of synchronization always occurred after the actual onset of movement. Moreover, in accordance with Alegre's study, we found that during action observation, the alpha/beta band ERD was especially marked during the effective experimenter's grasp. A peri-movement alpha/beta (6 – 11 Hz, 18 – 25 Hz) ERD was also observed in the GPi of patients with dystonia (Brücke et al., 2008). The above mentioned results found within the STN can be reasonably compared to those we found in the putamen in that the STN, likewise the putamen, is an input nucleus of the BG, and it is closely interconnected with cortical areas belonging to the MN network (Nambu et al., 2002). However, it is also important to note that these studies were all conduced on PD patients, that show altered electrophysiological changes in the BG, and therefore their results could, at least partially, reflect non-physiologic conditions.

Notably, the alpha/beta band modulations we observed during both action execution and observation, show striking similarities with the phenomenology of the cortical mu rhythm. The mu rhythm is an EEG oscillation, originating from the human sensorimotor cortex (Hari and Salmelin, 1997), with dominant frequencies in the alpha (8-13 Hz) and beta (15-25 Hz) bands (Hari and Salmelin, 1997; Pineda, 2005). This rhythm is enhanced during idling states (Pfurtscheller et al., 1996a) and suppressed during movement preparation and execution (Tremblay et al., 2004; Aridan et al., 2018), but also during action observation (Hari et al., 1998; Muthukumaraswamy et al., 2004; Tremblay et al., 2004) and motor imagery (Pfurtscheller et al., 2006a). The source of this rhythm and its phenomenology led to the hypothesis that it could indirectly reflect the activity of MNs (Pineda, 2005). Systematic intracortical LFP ERD within this frequency band in relation to action observation and execution were also observed in the monkey PMv (Caggiano et al., 2014; Kilner et al., 2014; Waldert et al., 2015) and M1 (Waldert et al., 2015). Confirming the similarity of modulations across the BG and the motor cortex, Alegre et al. (2010) observed that the LFP beta ERD in the STN was associated with a similar EEG modulation at the level of the motor cortex, suggesting a possible influence of cortical inputs on these subcortical rhythms, as also proposed by Marsden et al. (2001). Similar modulations across the STN and the motor cortex were also observed by previous studies (Alegre et al., 2005; Cassidy et al., 2002; Kühn et al. 2006). In light of these findings, authors speculated that beta ERD could be at least partially a consequence of the activation of the human MN network, supporting the hypothesis of a possible involvement of the BG in this network (Alegre et al., 2010). Due to the dense connections between the putamen nucleus and cortical areas active during both action execution and observation, similar neural oscillations at the two levels could convey motor and sensory information related to self and others' action across the basal ganglia-thalamocortical circuits. Finally, although the LFP modulations in this frequency band were similar for both action execution and observation, the presence of some differences in the two conditions raise the possibility that partially overlapping but nonidentical networks are active during action execution and observation.

We also observed a decreasing trend of the high-beta/low-gamma frequency band (26 – 40 Hz) during both action execution and observation. However, the phenomenology of this latter band appeared to be different from that of the alpha/beta band (9 – 15 Hz), being less marked and differently modulated by action execution and observation (with action execution associated with a progressive suppression during task unfolding and action observation characterized by a similar decreasing trend, but with a slight increase during

the pre-movement epoch). We are not aware of studies that investigated the modulation of this medium-high frequency band during action execution and/or observation in the BG, since most of them focused on the more prominent low beta modulations (Marceglia et al., 2009; Alegre et al., 2010; Malekmohammadi et al., 2019). However, a support of a distinction between these two frequency bands comes from a study on PD patients, showing an exaggerated activity in two distinct frequency bands (13 – 20 Hz and 20 – 35 Hz) in the motor territories of the BG, with activity in the lower band usually dominating over the power in the upper band (López-Azcárate et al., 2010). Another study (Priori et al., 2004) described a different response of these two bands in the STN of PD patients to anti-parkinsonian medications, suggesting that they could have a different functional meaning. Further studies are required to better understand the possible functional role of these medium-high frequency band oscillations.

Finally, with respect to the high frequency band (60 – 100 Hz), we found a clear synchronization starting from the pre-movement epoch and lasting throughout the grasping action in the execution condition. On the other hand, in the observation condition this ERS was mostly confined to the 500 ms following the experimenter's go cue. An ERS of the gamma band in relation to movement preparation and execution has been widely confirmed by several studies in the BG (Cassidy et al. 2002; DeCoteau et al., 2004; Alegre et al., 2005; Alegre et al., 2010), including the striatum (Masimore et al., 2005; Jenkinson et al., 2013), and in the motor cortex (Bimbi et al., 2018), leading to the hypothesis that this band is potentially critical for the organization of movements (Ulloa, 2022) as it better correlates with spiking output than with synaptic input (Ray et al., 2008). Moreover, the peri-movement gamma synchronization in the BG is coherent with cortical activity (at least in PD patients, see Cassidy et al. 2002). However, the relationship between these oscillations at the two levels is still poorly understood (Jenkinson, 2012). Our results could provide further support of the involvement of this frequency band in movement organization: indeed, the synchronization of this band was slightly anticipated in trials when reaction times were minimal compared to trials when they were maximal. However, this synchronization did not appear to be strictly related to overt movements: indeed, its peak occurred approximately within the 500 ms time interval following the go cue, regardless of whether the grasping action had already started or not. Rather, it seems to reflect a preparatory signal, regardless of its actual motor outcome. Finally, the observed ERS of the high gamma band during the pre-movement epoch in the action observation condition could be reconciled with a possible involvement of this band in inhibitory

responses (Ray et al., 2012). It could be speculated that the observed ERS of the gamma band in the execution condition might reflect the activation of the direct pathway, associated with facilitation of movement preparation, whereas the ERS observed in the observation condition might reflect the activation of the indirect pathway, associated with the suppression of movement preparation. A confirmation of this interpretation could be obtained by selectively blocking the D1 and D2 dopamine receptors - expressed by the direct and the indirect pathway, respectively - with dopamine antagonists and by investigating the possible presence of a selective reduction in the high gamma synchronization during either action execution or observation.

4.2 LFP Encoding of grip type

We also found the delta/theta band was differently modulated by the type of grip, with precision grip associated with a significantly higher ERS compared to whole hand prehension, for the action execution condition. The different modulation of delta/theta frequency band for the two grip types during epochs preceding the effective grasp in execution condition is consistent with the above mentioned possible functional role of this band in the selection of a choice during goal-directed behaviours, i.e., in our case, the selection of the correct grip type. Specifically a more enhanced ERS for the PG might reflect a higher complexity of the movement.

4.3 Limitations and future perspectives

While the neural basis of LFPs recorded in layered cortical structures is well established, we currently lack a clear mechanistic understanding of how LFPs are generated in non-laminar structures such as the BG, given that their anatomy is predicted to obstacle the generation of strong electric fields. It could be speculated that oscillations observed in the BG are not internally generated (do not reflect the activity of neurons around the electrode) but mostly represent a product of a volume conduction (i.e. of passive currents generated by neighbouring brain areas, see Boraud, 2005). Although we cannot completely rule out this alternative explanation, the use of high-impedance electrodes, together with the recent finding that the striatum is capable of generating an oscillatory activity by its own (Chartove et al., 2019), makes it likely that the recorded neural activity was local.

A possible limitation to our study is that we did not record the EMG activity of digit, hand and arm muscles, to exclude that the LFP modulation during sensory epochs of EXE conditions and during action observation could be explained by monkey's own movements. However, we obtained some degree of control

over this aspect, at least with regard to the movements of the hand contralateral to the recorded region. Indeed, a trial in the EXE conditions was considered correct and analysed if and only if the monkey kept the manipulandum pressed until the go cue in EXE conditions and throughout the duration of the trial in the OBS conditions (including the motor epoch during which the experimenter reached and grasped the target object): this did not only prevent overt preparation of reaching action, but actively required to keep tonically active an opposite motor plan to maintain the button pressed. Moreover, a study on nonhuman primates controlling for the occurrence of limb and hand movements (using chronically implanted electrodes in muscles) during an action observation task analogue to our own revealed that the inclusion or the exclusion of those trials in which muscle activity was detected did not revealed qualitative differences in the LFP modulation, but only small quantitative differences (Waldert et al., 2015). Finally, adopting the perspective of the social affordance hypothesis (Orban et al., 2021) that affirms the role of the encoding of others' observed actions in planning and preparing social interactions, the presence of an EMG activity during action observation would be irrelevant to the interpretation of our results.

Another possible limitation of the study is that we did not use an eye-tracking system that could detect the monkey's gaze direction. Therefore, we could not be certain that the monkey was actually watching the experimenter's grasping actions in OBS conditions. This latter aspect will have to be controlled in future studies, with either an eye-tracking system or an infrared camera. However, in a context in which the experimenter's action can be predicted, as in our case, the effective vision of the action is not strictly necessary to activate cortical MNs (Maranesi et al., 2014). Moreover, direct fixation by itself does not ensure the actual processing of the visual information.

A final consideration is that while the analysed sensory epochs included the time interval between the actual onset of the corresponding event (*Sound On, Oled On, Light On*) and the onset of the following event, on a trial by trial basis, the pre-movement epoch (*Sound Off*) was computed, for each trial, as the time interval between the go cue and the median time interval of the release of the manipulandum, calculated over all recording sessions separately for each. Therefore, modulations observed within this latter epoch are partially influenced by the actual executed or observed movement onset, and thus cannot be considered as strictly pre-motor, but rather reflect the neural activity during a transitional phase between the two events.

Future studies will have to provide a comprehensive view of LFP results here presented with single neuron signals previously obtained from the same animal (Rotunno et al. FENS 2022), showing evidence of single-units modulated during both action execution and observation. A relevant aspect to analyse could be the relationship and the interactions between LFP and single-unit activity simultaneously recorded from the same channels: investigating this aspects, and specifically the relationship between the single-units firing rates and the LFP phase and/or power, could help us better understand in which way the putamen nucleus represent information relative to one's own and others' observed actions. It would also be useful to simultaneously record and compare the LFP signal from the putamen and the connected cortical nodes of the MN network, to better understand the relationship between the neural oscillations at the two levels and the possible involvement of this nucleus in the extended MN network.

4.4 Conclusions

In conclusion, our results clearly illustrate that LFPs recorded from the macaque putamen are modulated by both action execution and observation of grasping actions. Neural oscillations within this nucleus, and specifically those in the alpha/beta band, could play a role in motor-based high-order social functions, including the encoding of others' observed actions. These findings underpin the hypothesis of the involvement of the BG in the extended MN network.

REFERENCES

Akins, P. T., Surmeier, D. J., & Kitai, S. T. (1990). Muscarinic modulation of a transient K+ conductance in rat neostriatal neurons. *Nature*, *344*(6263), 240-242. Doi: 10.1038/344240a0

Albin, R. L., Young, A. B., & Penney, J. B. (1989). The functional anatomy of basal ganglia disorders. *Trends in neurosciences*, *12*(10), 366-375. Doi: 10.1016/0166-2236(89)90074-x

Alegre, M., Alonso-Frech, F., Rodríguez-Oroz, M. C., Guridi, J., Zamarbide, I., Valencia, M., Manrique, M., Obeso, J. A., & Artieda, J. (2005). Movement-related changes in oscillatory activity in the human subthalamic nucleus: ipsilateral vs. contralateral movements. *The European journal of neuroscience*, *22*(9), 2315–2324. Doi: 10.1111/j.1460-9568.2005.04409.x

Alegre, M., Rodríguez-Oroz, M. C., Valencia, M., Pérez-Alcázar, M., Guridi, J., Iriarte, J., Obeso, J. A., & Artieda, J. (2010). Changes in subthalamic activity during movement observation in Parkinson's disease: is the mirror system mirrored in the basal ganglia?. *Clinical Neurophysiology*, *121*(3), 414-425. Doi: 10.1016/j.clinph.2009.11.013

Alexander G. E. (1987). Selective neuronal discharge in monkey putamen reflects intended direction of planned limb movements. *Experimental brain research*, *67*(3), 623–634. Doi: 10.1007/BF00247293

Alexander, G. E., & Crutcher, M. D. (1990a). Functional architecture of basal ganglia circuits: neural substrates of parallel processing. *Trends in neurosciences*, *13*(7), 266–271. Doi: 10.1016/0166-2236(90)90107-l

Alexander, G. E., & Crutcher, M. D. (1990b). Preparation for movement: neural representations of intended direction in three motor areas of the monkey. *Journal of neurophysiology*, *64*(1), 133–150. Doi: 10.1152/jn.1990.64.1.133

Alexander, G. E., & Crutcher, M. D. (1990c). Neural representations of the target (goal) of visually guided arm movements in three motor areas of the monkey. *Journal of neurophysiology*, *64*(1), 164–178. Doi: 10.1152/jn.1990.64.1.164

Alexander, G. E., Crutcher, M. D., & DeLong, M. R. (1991). Basal ganglia-thalamocortical circuits: parallel substrates for motor, oculomotor,"prefrontal" and "limbic" functions. *Progress in brain research*, *85*, 119-146. Doi: 10.1016/S0079-6123(08)62678-3

Alexander, G. E., & DeLong, M. R. (1985). Microstimulation of the primate neostriatum. II. Somatotopic organization of striatal microexcitable zones and their relation to neuronal response properties. *Journal of Neurophysiology*, *53*(6), 1417-1430. Doi: 10.1152/jn.1985.53.6.1417

Alexander, G. E., DeLong, M. R., & Strick, P. L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annual review of neuroscience*, *9*, 357–381. Doi: 10.1146/annurev.ne.09.030186.002041

Aosaki, T., Tsubokawa, H., Ishida, A., Watanabe, K., Graybiel, A. M., & Kimura, M. (1994). Responses of tonically active neurons in the primate's striatum undergo systematic changes during behavioral sensorimotor conditioning. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *14*(6), 3969–3984. Doi: 10.1523/JNEUROSCI.14-06-03969.1994

Aosaki, T., Kimura, M., & Graybiel, A. M. (1995). Temporal and spatial characteristics of tonically active neurons of the primate's striatum. *Journal of neurophysiology*, *73*(3), 1234-1252. Doi: 10.1152/jn.1995.73.3.1234

Apicella, P. (2002). Tonically active neurons in the primate striatum and their role in the processing of information about motivationally relevant events. *European Journal of Neuroscience*, *16*(11), 2017-2026. Doi: 10.1046/j.1460-9568.2002.02262.x

Aridan, N., Ossmy, O., Buaron, B., Reznik, D., & Mukamel, R. (2018). Suppression of EEG mu rhythm during action observation corresponds with subsequent changes in behavior. *Brain research*, *1691*, 55–63. Doi: 10.1016/j.brainres.2018.04.013

Baker, S. N., Olivier, E., & Lemon, R. N. (1997). Coherent oscillations in monkey motor cortex and hand muscle EMG show task-dependent modulation. *The Journal of physiology*, *501 (Pt 1)*(Pt 1), 225–241. Doi: 10.1111/j.1469-7793.1997.225bo.x

Barone, J., & Rossiter, H. E. (2021). Understanding the Role of Sensorimotor Beta Oscillations. *Frontiers in systems neuroscience*, *15*, 655886. Doi: 10.3389/fnsys.2021.655886

Belmalih, A., Borra, E., Contini, M., Gerbella, M., Rozzi, S., & Luppino, G. (2009). Multimodal architectonic subdivision of the rostral part (area F5) of the macaque ventral premotor cortex. *The Journal of comparative neurology*, *512*(2), 183–217. Doi: 10.1002/cne.21892

Bergman, H., Feingold, A., Nini, A., Raz, A., Slovin, H., Abeles, M., & Vaadia, E. (1998). Physiological aspects of information processing in the basal ganglia of normal and parkinsonian primates. *Trends in neurosciences*, *21*(1), 32-38. Doi: 10.1016/S0166-2236(97)01151-X

Berke J. D. (2009). Fast oscillations in cortical-striatal networks switch frequency following rewarding events and stimulant drugs. *The European journal of neuroscience*, *30*(5), 848–859. Doi: 10.1111/j.1460-9568.2009.06843.x

Berke, J. D. (2011). Functional properties of striatal fast-spiking interneurons. *Frontiers in systems neuroscience*, *5*, 45. Doi: 10.3389/fnsys

Berke, J. D. (2011). Functional properties of striatal fast-spiking interneurons. *Frontiers in systems neuroscience*, *5*, 45. Doi: 10.3389/fnsys

Berke, J. D., Okatan, M., Skurski, J., & Eichenbaum, H. B. (2004). Oscillatory entrainment of striatal neurons in freely moving rats. *Neuron*, *43*(6), 883-896. Doi: 10.1016/j.neuron.2004.08.035

Bevan, M. D., Magill, P. J., Terman, D., Bolam, J. P., & Wilson, C. J. (2002). Move to the rhythm: oscillations in the subthalamic nucleus-external globus pallidus network. *Trends in neurosciences*, *25*(10), 525–531. Doi: 10.1016/s0166-2236(02)02235-x

Bimbi, M., Festante, F., Coudé, G., Vanderwert, R. E., Fox, N. A., & Ferrari, P. F. (2018). Simultaneous scalp recorded EEG and local field potentials from monkey ventral premotor cortex during action observation and execution reveals the contribution of mirror and motor neurons to the mu-rhythm. *NeuroImage*, *175*, 22–31. Doi: 10.1016/j.neuroimage.2018.03.037

Bonini, L. (2017). The extended mirror neuron network: Anatomy, origin, and functions. *The Neuroscientist*, *23*(1), 56-67. Doi: 10.1177/1073858415626400

Bonini, L., & Ferrari, P. F. (2011). Evolution of mirror systems: a simple mechanism for complex cognitive functions. *Annals of the New York Academy of Sciences*, *1225*(1), 166–175. Doi: 10.1111/j.1749-6632.2011.06002.x

Bonini, L., Maranesi, M., Livi, A., Fogassi, L., & Rizzolatti, G. (2014). Space-dependent representation of objects and other's action in monkey ventral premotor grasping neurons. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *34*(11), 4108–4119. Doi: 10.1523/JNEUROSCI.4187-13.2014

Bonini, L., Rotunno, C., Arcuri, E., & Gallese, V. (2022). Mirror neurons 30 years later: implications and applications. *Trends in cognitive sciences*, *26*(9), 767–781. Doi: 10.1016/j.tics.2022.06.003

Boraud, T., Brown, P., Goldberg, J. A., Graybiel, A. M., & Magill, P. J. (2005). Oscillations in the basal ganglia: the good, the bad, and the unexpected. In *The basal ganglia VIII* (pp. 1-24). Springer, Boston, MA. Doi: 10.1007/0-387-28066-9_1

Borra, E., Belmalih, A., Calzavara, R., Gerbella, M., Murata, A., Rozzi, S., & Luppino, G. (2008). Cortical connections of the macaque anterior intraparietal (AIP) area. *Cerebral cortex (New York, N.Y. : 1991)*, *18*(5), 1094–1111. Doi: 10.1093/cercor/bhm146

Borra, E., Gerbella, M., Rozzi, S., & Luppino, G. (2017). The macaque lateral grasping network: A neural substrate for generating purposeful hand actions. *Neuroscience and biobehavioral reviews*, *75*, 65–90. Doi: 10.1016/j.neubiorev.2017.01.017

Brimblecombe, K. R., & Cragg, S. J. (2017). The striosome and matrix compartments of the striatum: a path through the labyrinth from neurochemistry toward function. *ACS chemical neuroscience*, *8*(2), 235-242. Doi: 10.1021/acschemneuro.6b00333

Brittain, J. S., & Brown, P. (2014). Oscillations and the basal ganglia: motor control and beyond. *NeuroImage*, *85 Pt 2*(Pt 2), 637–647. Doi: 10.1016/j.neuroimage.2013.05.084

Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues*. Barth.

Brown, P., Oliviero, A., Mazzone, P., Insola, A., Tonali, P., & Di Lazzaro, V. (2001). Dopamine dependency of oscillations between subthalamic nucleus and pallidum in Parkinson's disease. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *21*(3), 1033–1038. Doi: 10.1523/JNEUROSCI.21-03-01033.2001

Brücke, C., Kempf, F., Kupsch, A., Schneider, G. H., Krauss, J. K., Aziz, T., Yarrow, K., Pogosyan, A., Brown, P., & Kühn, A. A. (2008). Movement-related synchronization of gamma activity is lateralized in patients with dystonia. *The European journal of neuroscience*, *27*(9), 2322–2329. Doi: 10.1111/j.1460-9568.2008.06203.x

Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents--EEG, ECoG, LFP and spikes. *Nature reviews. Neuroscience*, *13*(6), 407–420. Doi: 10.1038/nrn3241

Caggiano, V., Giese, M., Thier, P., & Casile, A. (2015). Encoding of point of view during action observation in the local field potentials of macaque area F5. *The European journal of neuroscience*, *41*(4), 466–476. Doi: 10.1111/ejn.12793

Caligiore, D., Pezzulo, G., Miall, R. C., & Baldassarre, G. (2013). The contribution of brain sub-cortical loops in the expression and acquisition of action understanding abilities. *Neuroscience and biobehavioral reviews*, *37*(10 Pt 2), 2504–2515. Doi: 10.1016/j.neubiorev.2013.07.016

Carpenter, M. B., & Peter, P. (1972). Nigrostriatal and nigrothalamic fibers in the rhesus monkey. *The Journal of comparative neurology*, *144*(1), 93–115. Doi: 10.1002/cne.901440105

Casile, A., Caggiano, V., & Ferrari, P. F. (2011). The mirror neuron system: a fresh view. *The Neuroscientist: a review journal bringing neurobiology, neurology and psychiatry*, *17*(5), 524–538. Doi: 10.1177/1073858410392239

Cassidy, M., Mazzone, P., Oliviero, A., Insola, A., Tonali, P., Di Lazzaro, V., & Brown, P. (2002). Movement-related changes in synchronization in the human basal ganglia. *Brain : a journal of neurology*, *125*(Pt 6), 1235–1246. Doi: 10.1093/brain/awf135

Chang, H. T., Wilson, C. J., & Kitai, S. T. (1981). Single neostriatal efferent axons in the globus pallidus: a light and electron microscopic study. *Science (New York, N.Y.)*, *213*(4510), 915–918. Doi: 10.1126/science.7256286

Chartove, J. A. K., McCarthy, M. M., Pittman-Polletta, B. R., & Kopell, N. J. (2020). A biophysical model of striatal microcircuits suggests gamma and beta oscillations interleaved at delta/theta frequencies mediate periodicity in motor control. *PLoS computational biology*, *16*(2), e1007300. Doi: 10.1371/journal.pcbi.1007300

Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. (2014). Mirror neurons: from origin to function. *The Behavioral and brain sciences*, *37*(2), 177–192. Doi: 10.1017/S0140525X13000903

Corbit, L. H., & Balleine, B. W. (2011). The general and outcome-specific forms of Pavlovian-instrumental transfer are differentially mediated by the nucleus accumbens core and shell. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *31*(33), 11786–11794. Doi: 10.1523/JNEUROSCI.2711-11.2011

Courtemanche, R., Fujii, N., & Graybiel, A. M. (2003). Synchronous, focally modulated β-band oscillations characterize local field potential activity in the striatum of awake behaving monkeys. *Journal of Neuroscience*, *23*(37), 11741-11752. Doi: 10.1523/JNEUROSCI.23-37-11741.2003

Crutcher, M. D., & DeLong, M. R. (1984). Single cell studies of the primate putamen. I. Functional organization. *Experimental brain research*, *53*(2), 233–243. Doi: 10.1007/BF00238153

DeCoteau, W. E., Thorn, C., Gibson, D. J., Courtemanche, R., Mitra, P., Kubota, Y., & Graybiel, A. M. (2007). Oscillations of local field potentials in the rat dorsal striatum during spontaneous and instructed behaviors. *Journal of neurophysiology*, *97*(5), 3800-3805. Doi: 10.1152/jn.00108.2007

DeLong M. R. (1973). Putamen: activity of single units during slow and rapid arm movements. *Science (New York, N.Y.)*, *179*(4079), 1240–1242. Doi: 10.1126/science.179.4079.1240

DeLong, M. R., & Strick, P. L. (1974). Relation of basal ganglia, cerebellum, and motor cortex units to ramp and ballistic limb movements. *Brain research*, *71*(2-3), 327–335. Doi: 10.1016/0006-8993(74)90975-5

Destexhe, A., & Bédard, C. (2013). Local field potentials (LFP). In: Jaeger, D., Jung, R. (eds) *Encyclopedia of Computational Neuroscience*. Springer, New York, NY. Doi: 10.1007/978-1-4614-7320-6

Destexhe, A., Goldberg, J.A. (2015). LFP Analysis: Overview. In: Jaeger, D., Jung, R. (eds) *Encyclopedia of Computational Neuroscience*. Springer, New York, NY. Doi: 10.1007/978-1-4614-7320-6

Devinsky, O., Morrell, M. J., & Vogt, B. A. (1995). Contributions of anterior cingulate cortex to behaviour. *Brain: a journal of neurology*, *118 (Pt 1)*, 279–306. Doi: 10.1093/brain/118.1.279

DiFiglia, M. (1987). Synaptic organization of cholinergic neurons in the monkey neostriatum. *Journal of Comparative Neurology*, *255*(2), 245-258. Doi: 10.1002/cne.902550208

DiFiglia, M., Pasik, P., & Pasik, T. (1976). A Golgi study of neuronal types in the neostriatum of monkeys. *Brain research*, *114*(2), 245-256. Doi: 10.1016/0006-8993(76)90669-7

Ding, L., & Gold, J. I. (2010). Caudate encodes multiple computations for perceptual decisions. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *30*(47), 15747–15759. Doi: 10.1523/JNEUROSCI.2894-10.2010

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental brain research*, *91*(1), 176-180. Doi: 10.1007/BF00230027

Disbrow, E., Litinas, E., Recanzone, G. H., Padberg, J., & Krubitzer, L. (2003). Cortical connections of the second somatosensory area and the parietal ventral area in macaque monkeys. The Journal of comparative neurology, 462(4), 382–399. Doi: 10.1002/cne.10731

Divac, I., Fonnum, F., & Storm-Mathisen, J. (1977). High affinity uptake of glutamate in terminals of corticostriatal axons. *Nature*, *266*(5600), 377–378. Doi: 10.1038/266377a0

Dushanova, J., & Donoghue, J. (2010). Neurons in primary motor cortex engaged during action observation. *The European journal of neuroscience*, *31*(2), 386–398. Doi: 10.1111/j.1460-9568.2009.07067.x

Engel, A. K., & Fries, P. (2010). Beta-band oscillations - signalling the status quo?. *Current opinion in neurobiology*, *20*(2), 156-165. Doi: 10.1016/j.conb.2010.02.015

Ericsson, J., Stephenson-Jones, M., Pérez-Fernández, J., Robertson, B., Silberberg, G., & Grillner, S. (2013). Dopamine differentially modulates the excitability of striatal neurons of the direct and indirect pathways in lamprey. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *33*(18), 8045–8054. Doi: 10.1523/JNEUROSCI.5881-12.2013

Errante, A., & Fogassi, L. (2020). Activation of cerebellum and basal ganglia during the observation and execution of manipulative actions. *Scientific reports*, *10*(1), 12008. Doi: 10.1038/s41598-020-68928-w

Ferrari, P. F., & Coudé, G. (2018). Mirror neurons, embodied emotions, and empathy. In *Neuronal correlates of empathy* (pp. 67-77). Academic Press. Doi: 10.1016/B978-0-12-805397-3.00006-1

Ferrari, P. F., Gerbella, M., Coudé, G., & Rozzi, S. (2017). Two different mirror neuron networks: The sensorimotor (hand) and limbic (face) pathways. *Neuroscience*, *358*, 300–315. Doi: 10.1016/j.neuroscience.2017.06.052

Flaherty, A. W., & Graybiel, A. M. (1991). Corticostriatal transformations in the primate somatosensory system. Projections from physiologically mapped body-part representations. *Journal of neurophysiology*, *66*(4), 1249–1263. Doi: 10.1152/jn.1991.66.4.1249

Florio, T. M., Scarnati, E., Rosa, I., Di Censo, D., Ranieri, B., Cimini, A., Galante, A., & Alecci, M. (2018). The Basal Ganglia: More than just a switching device. *CNS neuroscience & therapeutics*, *24*(8), 677–684. Doi: 10.1111/cns.12987

Fogassi, L., & Ferrari, P. F. (2011). Mirror systems. *Wiley interdisciplinary reviews. Cognitive science*, *2*(1), 22–38. Doi: 10.1002/wcs.89

François, C., Percheron, G., Parent, A., Sadikot, A. F., Fenelon, G., & Yelnik, J. (1991). Topography of the projection from the central complex of the thalamus to the sensorimotor striatal territory in monkeys. *The Journal of comparative neurology*, *305*(1), 17–34. Doi: 10.1002/cne.903050104

Frederick, A., Bourget-Murray, J., Courtemanche, R., Local Field Potentials, Synchrony of. In: Jaeger, D., Jung, R. (eds) *Encyclopedia of Computational Neuroscience*. Springer, New York, NY. Doi: 10.1007/978-1-4614-7320-6

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G. (2002). Action representation and the inferior parietal lobule. In Prinz, W., Hommel, B. (eds.) Common Mechanisms in Perception and Action: Attention and Performance, Vol. XIX. Oxford: Oxford University Press, pp. 334-355.

Galvan, A., & Smith, Y. (2011). The primate thalamostriatal systems: Anatomical organization, functional roles and possible involvement in Parkinson's disease. *Basal ganglia*, *1*(4), 179–189. Doi: 10.1016/j.baga.2011.09.001

Gardiner, T. W., & Nelson, R. J. (1992). Striatal neuronal activity during the initiation and execution of hand movements made in response to visual and vibratory cues. *Experimental brain research*, *92*(1), 15–26. Doi: 10.1007/BF00230379

Gatev, P., Darbin, O., & Wichmann, T. (2006). Oscillations in the basal ganglia under normal conditions and in movement disorders. *Movement disorders: official journal of the Movement Disorder Society*, *21*(10), 1566–1577. Doi: 10.1002/mds.21033

Ge, S., Liu, H., Lin, P., Gao, J., Xiao, C., & Li, Z. (2018). Neural Basis of Action Observation and Understanding From First- and Third-Person Perspectives: An fMRI Study. *Frontiers in behavioral neuroscience*, *12*, 283. Doi: 10.3389/fnbeh.2018.00283

Gerbella, M., Borra, E., Mangiaracina, C., Rozzi, S., & Luppino, G. (2016). Corticostriate Projections from Areas of the "Lateral Grasping Network": Evidence for Multiple Hand-Related Input Channels. *Cerebral cortex (New York, N.Y.: 1991)*, *26*(7), 3096–3115. Doi: 10.1093/cercor/bhv135

Gerfen, C. R. (1988). Synaptic organization of the striatum. *Journal of electron microscopy technique*, *10*(3), 265-281. Doi: 10.1002/jemt.1060100305

Gibson, J. J., (1979). *Ecological Approach to Visual Perception*. Houghton Mifflin.

Gervasoni, D., Lin, S. C., Ribeiro, S., Soares, E. S., Pantoja, J., & Nicolelis, M. A. (2004). Global forebrain dynamics predict rat behavioral states and their transitions. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *24*(49), 11137–11147. Doi: 10.1523/JNEUROSCI.3524-04.2004

Graybiel A. M. (1998). The basal ganglia and chunking of action repertoires. *Neurobiology of learning and memory*, *70*(1-2), 119–136. Doi: 10.1006/nlme.1998.3843

Grillner, S., Robertson, B., & Stephenson-Jones, M. (2013). The evolutionary origin of the vertebrate basal ganglia and its role in action selection. *The Journal of physiology*, *591*(22), 5425-5431. Doi: 10.1113/jphysiol.2012.246660

Hari, R., & Salmelin, R. (1997). Human cortical oscillations: a neuromagnetic view through the skull. *Trends in neurosciences*, *20*(1), 44–49. Doi: 10.1016/S0166-2236(96)10065-5

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(25), 15061–15065. Doi: 10.1073/pnas.95.25.15061

Herreras O. (2016). Local Field Potentials: Myths and Misunderstandings. *Frontiers in neural circuits*, *10*, 101. Doi: 10.3389/fncir.2016.00101

Hihara, S., Taoka, M., Tanaka, M., & Iriki, A. (2015). Visual responsiveness of neurons in the secondary somatosensory area and its surrounding parietal operculum regions in awake macaque monkeys. *Cerebral Cortex*, *25*(11), 4535-4550. Doi: 10.1093/cercor/bhv095

Hikosaka, O., Takikawa, Y., & Kawagoe, R. (2000). Role of the basal ganglia in the control of purposive saccadic eye movements. *Physiological reviews*, *80*(3), 953–978. Doi: 10.1152/physrev.2000.80.3.953

Inase, M., Tokuno, H., Nambu, A., Akazawa, T., & Takada, M. (1999). Corticostriatal and corticosubthalamic input zones from the presupplementary motor area in the macaque monkey: comparison with the input zones from the supplementary motor area. *Brain research*, *833*(2), 191–201. Doi: 10.1016/s0006-8993(99)01531-0

Jenkinson, N., Kühn, A. A., & Brown, P. (2013). γ oscillations in the human basal ganglia. *Experimental neurology*, *245*, 72–76. Doi 10.1016/j.expneurol.2012.07.005

Johnson, T. N., & Rosvold, H. E. (1971). Topographic projections on the globus pallidus and the substantia nigra of selectively placed lesions in the precommissural caudate nucleus and putamen in the monkey. *Experimental neurology*, *33*(3), 584–596. Doi: 10.1016/0014-4886(71)90129-4

Jones, E. G., Coulter, J. D., Burton, H., & Porter, R. (1977). Cells of origin and terminal distribution of corticostriatal fibers arising in the sensory-motor cortex of monkeys. *The Journal of comparative neurology*, *173*(1), 53–80. Doi: 10.1002/cne.901730105

Kandel, E. R., Schwartz, J. H., Jessell, T. M., Siegelbaum, S., Hudspeth, A. J., & Mack, S. (Eds.). (2000). *Principles of neural science* (Vol. 4, pp. 1227-1246). New York: McGraw-hill.

Kemp, J. M., & Powell, T. P. S. (1970). The cortico-striate projection in the monkey. *Brain*, *93*(3), 525-546. Doi: 10.1093/brain/93.3.525

Kessler, K., Biermann-Ruben, K., Jonas, M., Siebner, H. R., Bäumer, T., Münchau, A., & Schnitzler, A. (2006). Investigating the human mirror neuron system by means of cortical synchronization during the imitation of biological movements. *Neuroimage*, *33*(1), 227-238. Doi: 10.1016/j.neuroimage.2006.06.014

Kilner, J. M., Kraskov, A., & Lemon, R. N. (2014). Do monkey F5 mirror neurons show changes in firing rate during repeated observation of natural actions?. *Journal of neurophysiology*, *111*(6), 1214–1226. Doi: 10.1152/jn.01102.2012

Kimura, M., Rajkowski, J., & Evarts, E. (1984). Tonically discharging putamen neurons exhibit set-dependent responses. *Proceedings of the National Academy of Sciences of the United States of America*, *81*(15), 4998–5001. Doi: 10.1073/pnas.81.15.4998

Kimura M. (1986). The role of primate putamen neurons in the association of sensory stimuli with movement. *Neuroscience research*, *3*(5), 436–443. Doi: 10.1016/0168-0102(86)90035-0

Kimura M. (1990). Behaviorally contingent property of movement-related activity of the primate putamen. *Journal of neurophysiology*, *63*(6), 1277–1296. Doi: 10.1152/jn.1990.63.6.1277

Kilavik, B. E., Zaepffel, M., Brovelli, A., MacKay, W. A., & Riehle, A. (2013). The ups and downs of β oscillations in sensorimotor cortex. *Experimental neurology*, *245*, 15–26. Doi: 10.1016/j.expneurol.2012.09.014

Koralek, A. C., Long, J. D., Costa, R. M., & Carmena, J. M. (2010). Corticostriatal dynamics during learning and performance of a neuroprosthetic task. *Annual International Conference of the IEEE Engineering in*

Medicine and Biology Society. IEEE Engineering in Medicine and Biology Society. Annual International Conference, *2010*, 2682–2685. Doi: 10.1109/IEMBS.2010.5626632

Kreiman, G., Hung, C. P., Kraskov, A., Quiroga, R. Q., Poggio, T., & DiCarlo, J. J. (2006). Object selectivity of local field potentials and spikes in the macaque inferior temporal cortex. *Neuron*, *49*(3), 433–445. Doi: 10.1016/j.neuron.2005.12.019

Kühn, A. A., Kupsch, A., Schneider, G. H., & Brown, P. (2006). Reduction in subthalamic 8-35 Hz oscillatory activity correlates with clinical improvement in Parkinson's disease. *The European journal of neuroscience*, *23*(7), 1956–1960. Doi: 10.1111/j.1460-9568.2006.04717.x

Kühn, A. A., Trottenberg, T., Kivi, A., Kupsch, A., Schneider, G. H., & Brown, P. (2005). The relationship between local field potential and neuronal discharge in the subthalamic nucleus of patients with Parkinson's disease. *Experimental neurology*, *194*(1), 212–220. Doi: 10.1016/j.expneurol.2005.02.010

Künzle H. (1975). Bilateral projections from precentral motor cortex to the putamen and other parts of the basal ganglia. An autoradiographic study in Macaca fascicularis. *Brain research*, *88*(2), 195–209. Doi: 10.1016/0006-8993(75)90384-4

Künzle, H. (1977). Projections from the primary somatosensory cortex to basal ganglia and thalamus in the monkey. *Experimental Brain Research*, *30*(4), 481-492. Doi: 10.1007/BF00237639

Kurata, K., & Hoffman, D. S. (1994). Differential effects of muscimol microinjection into dorsal and ventral aspects of the premotor cortex of monkeys. *Journal of neurophysiology*, *71*(3), 1151–1164. Doi: 10.1152/jn.1994.71.3.1151

Lanciego, J. L., Luquin, N., & Obeso, J. A. (2012). Functional neuroanatomy of the basal ganglia. *Cold Spring Harbor perspectives in medicine*, *2*(12), a009621. Doi: 10.1101/cshperspect.a009621

Lanzilotto, M., Ferroni, C. G., Livi, A., Gerbella, M., Maranesi, M., Borra, E., Passarelli, L., Gamberini, M., Fogassi, L., Bonini, L., & Orban, G. A. (2019). Anterior Intraparietal Area: A Hub in the Observed Manipulative Action Network. *Cerebral cortex (New York, N.Y.: 1991)*, *29*(4), 1816–1833. Doi: 10.1093/cercor/bhz011

Levy, R., Ashby, P., Hutchison, W. D., Lang, A. E., Lozano, A. M., & Dostrovsky, J. O. (2002). Dependence of subthalamic nucleus oscillations on movement and dopamine in Parkinson's disease. *Brain: a journal of neurology*, *125*(Pt 6), 1196–1209. Doi: 10.1093/brain/awf128

Levy, R., Friedman, H. R., Davachi, L., & Goldman-Rakic, P. S. (1997). Differential activation of the caudate nucleus in primates performing spatial and nonspatial working memory tasks. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *17*(10), 3870–3882. Doi: 10.1523/JNEUROSCI.17-10-03870.1997

Liles S. L. (1983). Activity of neurons in the putamen associated with wrist movements in the monkey. *Brain research*, *263*(1), 156–161. Doi: 10.1016/0006-8993(83)91214-3

Little, S., Pogosyan, A., Kuhn, A. A., & Brown, P. (2012). β band stability over time correlates with Parkinsonian rigidity and bradykinesia. *Experimental neurology*, *236*(2), 383–388. Doi: 10.1016/j.expneurol.2012.04.024

Livi, A., Lanzilotto, M., Maranesi, M., Fogassi, L., Rizzolatti, G., & Bonini, L. (2019). Agent-based representations of objects and actions in the monkey pre-supplementary motor area. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(7), 2691–2700. Doi: 10.1073/pnas.1810890116

López-Azcárate, J., Tainta, M., Rodríguez-Oroz, M. C., Valencia, M., González, R., Guridi, J., Iriarte, J., Obeso, J. A., Artieda, J., & Alegre, M. (2010). Coupling between beta and high-frequency activity in the human subthalamic nucleus may be a pathophysiological mechanism in Parkinson's disease. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *30*(19), 6667–6677. Doi: 10.1523/JNEUROSCI.5459-09.2010

Luppino, G., & Rizzolatti, G. (2000). The Organization of the Frontal Motor Cortex. *News in physiological sciences: an international journal of physiology produced jointly by the International Union of Physiological Sciences and the American Physiological Society*, *15*, 219–224. Doi: 10.1152/physiologyonline.2000.15.5.219

Malekmohammadi, M., Cross, K., Choi, J., & Pouratian, N. (2019). Action Observation and Execution Differentially Modulate Basal Ganglia-Cortical Activity in Humans. *Neurosurgery*, *66*, 310-205. Doi: 10.1093/neuros/nyz310_205

Mannella, F., Gurney, K., & Baldassarre, G. (2013). The nucleus accumbens as a nexus between values and goals in goal-directed behavior: a review and a new hypothesis. *Frontiers in behavioral neuroscience*, *7*, 135. Doi: 10.3389/fnbeh.2013.00135

Maranesi, M., Bonini, L., & Fogassi, L. (2014). Cortical processing of object affordances for self and others' action. *Frontiers in psychology*, *5*, 538. Doi: 10.3389/fpsyg.2014.00538

Maranesi, M., Livi, A., Fogassi, L., Rizzolatti, G., & Bonini, L. (2014). Mirror neuron activation prior to action observation in a predictable context. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *34*(45), 14827–14832. Doi: 10.1523/JNEUROSCI.2705-14.2014

Marceglia, S., Fiorio, M., Foffani, G., Mrakic-Sposta, S., Tiriticco, M., Locatelli, M., Caputo, E., Tinazzi, M., & Priori, A. (2009). Modulation of beta oscillations in the subthalamic area during action observation in Parkinson's disease. *Neuroscience*, *161*(4), 1027–1036. Doi: 10.1016/j.neuroscience.2009.04.018

Marsden, J. F., Limousin-Dowsey, P., Ashby, P., Pollak, P., & Brown, P. (2001). Subthalamic nucleus, sensorimotor cortex and muscle interrelationships in Parkinson's disease. *Brain: a journal of neurology*, *124*(Pt 2), 378–388. Doi: 10.1093/brain/124.2.378

Masimore, B., Kakalios, J., & Redish, A. D. (2004). Measuring fundamental frequencies in local field potentials. *Journal of neuroscience methods*, *138*(1-2), 97–105. Doi: 10.1016/j.jneumeth.2004.03.014

Masimore, B., Schmitzer-Torbert, N. C., Kakalios, J., & Redish, A. D. (2005). Transient striatal gamma local field potentials signal movement initiation in rats. *Neuroreport*, *16*(18), 2021–2024. Doi: 10.1097/00001756-200512190-00010

Matelli, M., Luppino, G., & Rizzolatti, G. (1985). Patterns of cytochrome oxidase activity in the frontal agranular cortex of the macaque monkey. *Behavioural brain research*, *18*(2), 125–136. Doi: 10.1016/0166-4328(85)90068-3

Mathai, A., & Smith, Y. (2011). The corticostriatal and corticosubthalamic pathways: two entries, one target. So what?. *Frontiers in systems neuroscience*, *5*, 64. Doi: 10.3389/fnsys.2011.00064

Mazzoni, A., Lindén, H., Cuntz, H., Lansner, A., Panzeri, S., & Einevoll, G. T. (2015). Computing the local field potential (LFP) from integrate-and-fire network models. *PLoS computational biology*, *11*(12), e1004584. Doi: 10.1371/journal.pcbi.1004584

McCairn, K. W., Bronfeld, M., Belelovsky, K., & Bar-Gad, I. (2009). The neurophysiological correlates of motor tics following focal striatal disinhibition. *Brain: a journal of neurology*, *132*(Pt 8), 2125–2138. Doi: 10.1093/brain/awp142

McFarland, N. R., & Haber, S. N. (2000). Convergent inputs from thalamic motor nuclei and frontal cortical areas to the dorsal striatum in the primate. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *20*(10), 3798–3813. Doi: 10.1523/JNEUROSCI.20-10-03798.2000

Miller E. K. (2000). The prefrontal cortex and cognitive control. *Nature reviews. Neuroscience*, *1*(1), 59–65. Doi: 10.1038/35036228

Mink J. W. (1996). The basal ganglia: focused selection and inhibition of competing motor programs. *Progress in neurobiology*, *50*(4), 381–425. Doi: 10.1016/s0301-0082(96)00042-1

Mitzdorf, U. (1985). Current source-density method and application in cat cerebral cortex: investigation of evoked potentials and EEG phenomena. *Physiological reviews*, *65*(1), 37-100. Doi: 10.1152/physrev.1985.65.1.37

Moënne-Loccoz, C., Astudillo-Valenzuela, C., Skovgård, K., Salazar-Reyes, C. A., Barrientos, S. A., García-Núñez, X. P., Cenci, M. A., Petersson, P., & Fuentes-Flores, R. A. (2020). Cortico-Striatal Oscillations Are Correlated to Motor Activity Levels in Both Physiological and Parkinsonian Conditions. *Frontiers in systems neuroscience*, *14*, 56. Doi: 10.3389/fnsys.2020.00056

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2009). Is the mirror neuron system involved in imitation? A short review and meta-analysis. *Neuroscience and biobehavioral reviews*, *33*(7), 975–980. Doi: 10.1016/j.neubiorev.2009.03.010

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: a meta-analysis of 125 human fMRI studies. *Neuroscience and biobehavioral reviews*, *36*(1), 341–349. Doi: 10.1016/j.neubiorev.2011.07.004

Monakow, K. H., Akert, K., & Künzle, H. (1978). Projections of the precentral motor cortex and other cortical areas of the frontal lobe to the subthalamic nucleus in the monkey. *Experimental brain research*, *33*(3-4), 395–403. Doi: 10.1007/BF00235561

Montaron, M. F., Deniau, J. M., Menetrey, A., Glowinski, J., & Thierry, A. M. (1996). Prefrontal cortex inputs of the nucleus accumbens-nigro-thalamic circuit. *Neuroscience*, *71*(2), 371–382. Doi: 10.1016/0306-4522(95)00455-6

Mooney R. (2014). Auditory-vocal mirroring in songbirds. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *369*(1644), 20130179. Doi: 10.1098/rstb.2013.0179

Moore, R. Y., Bhatnagar, R. K., & Heller, A. (1971). Anatomical and chemical studies of a nigro-neostriatal projection in the cat. *Brain research*, *30*(1), 119-135. Doi: 10.1016/0006-8993(71)90009-6

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current biology*, *20*(8), 750–756. Doi: 10.1016/j.cub.2010.02.045

Müller, E. J., & Robinson, P. A. (2018). Suppression of Parkinsonian Beta Oscillations by Deep Brain Stimulation: Determination of Effective Protocols. *Frontiers in computational neuroscience*, *12*, 98. Doi: 10.3389/fncom.2018.00098

Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (area F5) of the monkey. *Journal of neurophysiology*, *78*(4), 2226–2230. Doi: 10.1152/jn.1997.78.4.2226

Murthy, V. N., & Fetz, E. E. (1992). Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(12), 5670–5674. Doi: 10.1073/pnas.89.12.5670

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Brain research. Cognitive brain research*, *19*(2), 195–201. Doi: 10.1016/j.cogbrainres.2003.12.001

Nácher, V., Ledberg, A., Deco, G., & Romo, R. (2013). Coherent delta-band oscillations between cortical areas correlate with decision making. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(37), 15085–15090. Doi: 10.1073/pnas.1314681110

Nambu A. (2004). A new dynamic model of the cortico-basal ganglia loop. *Progress in brain research*, *143*, 461–466. Doi: 10.1016/S0079-6123(03)43043-4

Nambu A. (2011). Somatotopic organization of the primate Basal Ganglia. *Frontiers in neuroanatomy*, *5*, 26. Doi: 10.3389/fnana.2011.00026

Nambu, A., Kaneda, K., Tokuno, H., & Takada, M. (2002a). Organization of corticostriatal motor inputs in monkey putamen. *Journal of Neurophysiology*, *88*(4), 1830-1842. Doi: 10.1152/jn.2002.88.4.1830

Nambu, A., Tokuno, H., & Takada, M. (2002b). Functional significance of the cortico–subthalamo–pallidal 'hyperdirect'pathway. *Neuroscience research*, *43*(2), 111-117. Doi: 10.1016/s0168-0102(02)00027-5

Nambu A. (2011). Somatotopic organization of the primate Basal Ganglia. *Frontiers in neuroanatomy*, *5*, 26. Doi: 10.3389/fnana.2011.00026

Nicola, S. M., Hopf, F. W., & Hjelmstad, G. O. (2004). Contrast enhancement: a physiological effect of striatal dopamine?. *Cell and tissue research*, *318*(1), 93–106. Doi: 10.1007/s00441-004-0929-z

Oliveri, M. (2018). Sistema extrapiramidale. In A. Maravita (a cura di), *Fondamenti anatomofisiologici della attività psichica* (pp. 184-191). Poletto.

Orban, G. A., Lanzilotto, M., & Bonini, L. (2021). From Observed Action Identity to Social Affordances. *Trends in cognitive sciences*, *25*(6), 493–505. Doi: 10.1016/j.tics.2021.02.012

Penfield, W., & Rasmussen, T. (1950). The cerebral cortex of man; a clinical study of localization of function.

Pani, P., Theys, T., Romero, M. C., & Janssen, P. (2014). Grasping execution and grasping observation activity of single neurons in the macaque anterior intraparietal area. *Journal of cognitive neuroscience*, *26*(10), 2342–2355. Doi: 10.1162/jocn_a_00647

Papadourakis, V., & Raos, V. (2019). Neurons in the Macaque Dorsal Premotor Cortex Respond to Execution and Observation of Actions. *Cerebral cortex (New York, N.Y.: 1991)*, *29*(10), 4223–4237. Doi: 10.1093/cercor/bhy304

Parent, A., Mackey, A., & De Bellefeuille, L. (1983). The subcortical afferents to caudate nucleus and putamen in primate: a fluorescence retrograde double labeling study. *Neuroscience*, *10*(4), 1137-1150. Doi: 10.1016/0306-4522(83)90104-5

Percheron, G., François, C., Yelnik, J., Fénelon, G., & Talbi, B. (1994). The basal ganglia related system of primates: definition, description and informational analysis. In *The basal ganglia IV* (pp. 3-20). Springer, Boston, MA. Doi: 10.1007/978-1-4613-0485-2_1

Perrett, D. I., Harries, M. H., Bevan, R., Thomas, S., Benson, P. J., Mistlin, A. J., Chitty, A. J., Hietanen, J. K., & Ortega, J. E. (1989). Frameworks of analysis for the neural representation of animate objects and actions. *The Journal of experimental biology*, *146*, 87–113. Doi: 10.1242/jeb.146.1.87

Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *The Journal of comparative neurology*, *228*(1), 105–116. Doi: 10.1002/cne.902280110

Pfurtscheller, G., Stancák, A., Jr, & Neuper, C. (1996a). Event-related synchronization (ERS) in the alpha band--an electrophysiological correlate of cortical idling: a review. *International journal of psychophysiology: official journal of the International Organization of Psychophysiology*, *24*(1-2), 39–46. Doi: 10.1016/s0167-8760(96)00066-9

Pfurtscheller, G., Stancák, A., Jr, & Neuper, C. (1996b). Post-movement beta synchronization. A correlate of an idling motor area?. *Electroencephalography and clinical neurophysiology*, *98*(4), 281–293. Doi: 10.1016/0013-4694(95)00258-8

Pineda J. A. (2005). The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". Brain research. Brain research reviews, 50(1), 57–68. Doi: 10.1016/j.brainresrev.2005.04.005

Popescu, A. T., Popa, D., & Paré, D. (2009). Coherent gamma oscillations couple the amygdala and striatum during learning. *Nature neuroscience*, *12*(6), 801–807. Doi: 10.1038/nn.2305

Prather, J. F., Peters, S., Nowicki, S., & Mooney, R. (2008). Precise auditory-vocal mirroring in neurons for learned vocal communication. *Nature*, *451*(7176), 305–310. Doi: 10.1038/nature06492

Preston, R. J., Bishop, G. A., & Kitai, S. T. (1980). Medium spiny neuron projection from the rat striatum: an intracellular horseradish peroxidase study. *Brain research*, *183*(2), 253–263. Doi: 10.1016/0006-8993(80)90462-x

Priori, A., Foffani, G., Pesenti, A., Tamma, F., Bianchi, A. M., Pellegrini, M., Locatelli, M., Moxon, K. A., & Villani, R. M. (2004). Rhythm-specific pharmacological modulation of subthalamic activity in Parkinson's disease. *Experimental neurology*, *189*(2), 369–379. Doi: 10.1016/j.expneurol.2004.06.001

Ravizza, S. M., & Ivry, R. B. (2001). Comparison of the basal ganglia and cerebellum in shifting attention. *Journal of cognitive neuroscience*, *13*(3), 285–297. Doi: 10.1162/08989290151137340

Ray, N. J., Brittain, J. S., Holland, P., Joundi, R. A., Stein, J. F., Aziz, T. Z., & Jenkinson, N. (2012). The role of the subthalamic nucleus in response inhibition: evidence from local field potential recordings in the human subthalamic nucleus. *NeuroImage*, *60*(1), 271–278. Doi: 10.1016/j.neuroimage.2011.12.035

Ray, S., Crone, N. E., Niebur, E., Franaszczuk, P. J., & Hsiao, S. S. (2008). Neural correlates of high-gamma oscillations (60-200 Hz) in macaque local field potentials and their potential implications in electrocorticography. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *28*(45), 11526–11536. Doi: 10.1523/JNEUROSCI.2848-08.2008

Reep, R. L., Cheatwood, J. L., & Corwin, J. V. (2003). The associative striatum: organization of cortical projections to the dorsocentral striatum in rats. *The Journal of comparative neurology*, *467*(3), 271–292. Doi: 10.1002/cne.10868

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in neurosciences*, *21*(5), 188–194. Doi: 10.1016/s0166-2236(98)01260-0

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive brain research*, *3*(2), 131-141. Doi: 10.1016/0926-6410(95)00038-0

Rizzolatti, G., Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., & Ponzoni-Maggi, S. (1987). Neurons related to goal-directed motor acts in inferior area 6 of the macaque monkey. *Experimental brain research*, *67*(1), 220–224. Doi: 10.1007/BF00269468

Rizzolatti, G., Luppino, G., & Matelli, M. (1998). The organization of the cortical motor system: new concepts. *Electroencephalography and clinical neurophysiology*, *106*(4), 283–296. Doi: 10.1016/s0013-4694(98)00022-4

Rizzolatti, G., Sinigaglia, C. (2006). *So quel che fai: il cervello che agisce ei neuroni specchio*. Milano: R. Cortina.

Romanelli, P., Esposito, V., Schaal, D. W., & Heit, G. (2005). Somatotopy in the basal ganglia: experimental and clinical evidence for segregated sensorimotor channels. *Brain research. Brain research reviews*, *48*(1), 112–128. Doi: 10.1016/j.brainresrev.2004.09.008

Rosa, M., Marceglia, S., Barbieri, S., Priori, A. (2015). Local Field Potential and Deep Brain Stimulation (DBS). In: Jaeger, D., Jung, R. (eds) *Encyclopedia of Computational Neuroscience*. Springer, New York, NY. Doi: 10.1007/978-1-4614-7320-6

Rotunno, C., Maranesi, M., Ferroni, C.G., Di Volo, M., Reni, M., Bonini, L. (2022). Neuronal representations of self and other's action in the monkey basal ganglia. FENS Forum 2022. https://kenesvm.azureedge.net/public/general/FENS2022.pdf

Rozzi, S., Ferrari, P. F., Bonini, L., Rizzolatti, G., & Fogassi, L. (2008). Functional organization of inferior parietal lobule convexity in the macaque monkey: electrophysiological characterization of motor, sensory and mirror responses and their correlation with cytoarchitectonic areas. *The European journal of neuroscience*, *28*(8), 1569–1588. Doi: 10.1111/j.1460-9568.2008.06395.x

Sadikot, A. F., Parent, A., Smith, Y., & Bolam, J. P. (1992). Efferent connections of the centromedian and parafascicular thalamic nuclei in the squirrel monkey: a light and electron microscopic study of the

thalamostriatal projection in relation to striatal heterogeneity. *The Journal of comparative neurology*, *320*(2), 228–242. Doi: 10.1002/cne.903200207

Salenius, S., Salmelin, R., Neuper, C., Pfurtscheller, G., & Hari, R. (1996). Human cortical 40 Hz rhythm is closely related to EMG rhythmicity. *Neuroscience letters*, *213*(2), 75–78. Doi: 10.1016/0304-3940(96)12796-8

Sanes, J. N., & Donoghue, J. P. (1993). Oscillations in local field potentials of the primate motor cortex during voluntary movement. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(10), 4470–4474. Doi: 10.1073/pnas.90.10.4470

Schroll, H., & Hamker, F. H. (2013). Computational models of basal-ganglia pathway functions: focus on functional neuroanatomy. *Frontiers in systems neuroscience*, *7*, 122. Doi: 10.3389/fnsys.2013.00122

Schultz, W., & Dickinson, A. (2000). Neuronal coding of prediction errors. *Annual review of neuroscience*, *23*, 473–500. Doi: 10.1146/annurev.neuro.23.1.473

Seltzer, B., & Pandya, D. N. (1994). Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer study. *The Journal of comparative neurology*, *343*(3), 445–463. Doi: 10.1002/cne.903430308

Sochurkova, D., & Rektor, I. (2003). Event-related desynchronization/synchronization in the putamen. An SEEG case study. *Experimental brain research*, *149*(3), 401-404. Doi: 10.1007/s00221-003-1371-2

Smith, Y., Shink, E., & Sidibe, M. (1998). Neuronal circuitry and synaptic connectivity of the basal ganglia. *Neurosurgery Clinics of North America*, *9*(2), 203-222. Doi: 10.1016/s1042-3680(18)30260-2

Somogyi, P., & Smith, A. D. (1979). Projection of neostriatal spiny neurons to the substantia nigra. Application of a combined Golgi-staining and horse-radish peroxidase transport procedure at both light and electron microscopic levels. *Brain research*, *178*(1), 3-15. Doi: 10.1016/0006-8993(79)90084-2

Taira, M., Mine, S., Georgopoulos, A. P., Murata, A., & Sakata, H. (1990). Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Experimental brain research*, *83*(1), 29–36. Doi: 10.1007/BF00232190

Takada, M., Tokuno, H., Hamada, I., Inase, M., Ito, Y., Imanishi, M., Hasegawa, N., Akazawa, T., Hatanaka, N., & Nambu, A. (2001). Organization of inputs from cingulate motor areas to basal ganglia in macaque monkey. *The European journal of neuroscience*, *14*(10), 1633–1650. Doi: 10.1046/j.0953-816x.2001.01789.x

Takada, M., Tokuno, H., Nambu, A., & Inase, M. (1998). Corticostriatal projections from the somatic motor areas of the frontal cortex in the macaque monkey: segregation versus overlap of input zones from the primary motor cortex, the supplementary motor area, and the premotor cortex. *Experimental brain research*, *120*(1), 114-128. Doi: 10.1007/s002210050384

Takakusaki, K., Habaguchi, T., Ohtinata-Sugimoto, J., Saitoh, K., & Sakamoto, T. (2003). Basal ganglia efferents to the brainstem centers controlling postural muscle tone and locomotion: a new concept for understanding motor disorders in basal ganglia dysfunction. *Neuroscience*, *119*(1), 293-308. Doi: 10.1016/s0306-4522(03)00095-2

Tepper, J. M., Abercrombie, E. D., & Bolam, J. P. (2007). Basal ganglia macrocircuits. *Progress in brain research*, *160*, 3-7. Doi: 10.1016/S0079-6123(06)60001-0

Tokuno, H., Inase, M., Nambu, A., Akazawa, T., Miyachi, S., & Takada, M. (1999). Corticostriatal projections from distal and proximal forelimb representations of the monkey primary motor cortex. *Neuroscience letters*, *269*(1), 33–36. Doi: 10.1016/s0304-3940(99)00401-2

Tort, A. B., Kramer, M. A., Thorn, C., Gibson, D. J., Kubota, Y., Graybiel, A. M., & Kopell, N. J. (2008). Dynamic cross-frequency couplings of local field potential oscillations in rat striatum and hippocampus during performance of a T-maze task. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(51), 20517–20522. Doi: 10.1073/pnas.0810524105

Tremblay, C., Robert, M., Pascual-Leone, A., Lepore, F., Nguyen, D. K., Carmant, L., Bouthillier, A., & Théoret, H. (2004). Action observation and execution: intracranial recordings in a human subject. *Neurology*, *63*(5), 937–938. Doi: 10.1212/01.wnl.0000137111.16767.c6

Ueda, Y., & Kimura, M. (2003). Encoding of direction and combination of movements by primate putamen neurons. *The European journal of neuroscience*, *18*(4), 980–994. Doi: 10.1046/j.1460-9568.2003.02814.x

Ulloa J. L. (2022). The Control of Movements via Motor Gamma Oscillations. *Frontiers in human neuroscience*, *15*, 787157. Doi: 10.3389/fnhum.2021.787157

Utter, A. A., & Basso, M. A. (2008). The basal ganglia: an overview of circuits and function. *Neuroscience & Biobehavioral Reviews*, *32*(3), 333-342. Doi: 10.1016/j.neubiorev.2006.11.003

Van Vleet, T. M., Burcham, K. J., Corwin, J. V., & Reep, R. L. (2000). Unilateral destruction of the medial agranular cortical projection zone in the dorsocentral striatum produces severe neglect in rats. *Psychobiology*, *28*(1), 57-66. Doi: 10.3758/BF03330629

Vicente, A. F., Bermudez, M. A., Romero, M., Perez, R., & Gonzalez, F. (2012). Putamen neurons process both sensory and motor information during a complex task. *Brain research*, *1466*, 70–81. Doi: 10.1016/j.brainres.2012.05.037

Von Stein, A., & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. *International journal of psychophysiology : official journal of the International Organization of Psychophysiology*, *38*(3), 301–313. Doi: 10.1016/s0167-8760(00)00172-0

Waldert, S., Vigneswaran, G., Philipp, R., Lemon, R. N., & Kraskov, A. (2015). Modulation of the Intracortical LFP during Action Execution and Observation. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *35*(22), 8451–8461. Doi: 10.1523/JNEUROSCI.5137-14.2015

Wang, J., Zhang, J. R., Zang, Y. F., & Wu, T. (2018). Consistent decreased activity in the putamen in Parkinson's disease: a meta-analysis and an independent validation of resting-state fMRI. *GigaScience*, *7*(6), giy071. Doi: 10.1093/gigascience/giy071

Wilson, C. J., Chang, H. T., & Kitai, S. T. (1990). Firing patterns and synaptic potentials of identified giant aspiny interneurons in the rat neostriatum. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *10*(2), 508–519. Doi: 10.1523/JNEUROSCI.10-02-00508.1990

Wilson, C. J., & Groves, P. M. (1981). Spontaneous firing patterns of identified spiny neurons in the rat neostriatum. *Brain research*, *220*(1), 67-80. Doi: 10.1016/0006-8993(81)90211-0

Womelsdorf, T., Vinck, M., Leung, L. S., & Everling, S. (2010). Selective theta-synchronization of choice-relevant information subserves goal-directed behavior. *Frontiers in human neuroscience*, *4*, 210. Doi: 10.3389/fnhum.2010.00210

Woolsey, C. N., Settlage, P. H., Meyer, D. R., Sencer, W., Pinto Hamuy, T., & Travis, A. M. (1952). Patterns of localization in precentral and "supplementary" motor areas and their relation to the concept of a premotor area. *Research publications - Association for Research in Nervous and Mental Disease*, *30*, 238–264.

Yamada, H., Fujimoto, K., & Yoshida, M. (1995). Neuronal mechanism underlying dystonia induced by bicuculline injection into the putamen of the cat. *Brain research*, *677*(2), 333–336. Doi: 10.1016/0006-8993(95)00190-2

Yeterian, E. H., & Van Hoesen, G. W. (1978). Cortico-striate projections in the rhesus monkey: the organization of certain cortico-caudate connections. *Brain research*, *139*(1), 43–63. Doi: 10.1016/0006-8993(78)90059-8

Yin, H. H., & Knowlton, B. J. (2006). The role of the basal ganglia in habit formation. *Nature reviews. Neuroscience*, *7*(6), 464–476. Doi: 10.1038/nrn1919

Yoshida, K., Saito, N., Iriki, A., & Isoda, M. (2011). Representation of others' action by neurons in monkey medial frontal cortex. *Current biology : CB*, *21*(3), 249–253. Doi: 10.1016/j.cub.2011.01.004