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## PALEONTOLOGY

# Semiaquatic adaptations in a giant predatory dinosaur

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We describe adaptations for a semiaquatic lifestyle in the dinosaur *Spinosaurus aegyptiacus*. These adaptations include retraction of the fleshy nostrils to a position near the mid-region of the skull and an elongate neck and trunk that shift the center of body mass anterior to the knee joint. Unlike terrestrial theropods, the pelvic girdle is downsized, the hindlimbs are short, and all of the limb bones are solid without an open medullary cavity, for buoyancy control in water. The short, robust femur with hypertrophied flexor attachment and the low, flat-bottomed pedal claws are consistent with aquatic foot-propelled locomotion. Surface striations and bone microstructure suggest that the dorsal “sail” may have been enveloped in skin that functioned primarily for display on land and in water.

**B**ones of the predatory dinosaur *Spinosaurus aegyptiacus* first came to light over a century ago from Upper Cretaceous rocks in Egypt (1–3) but were destroyed in World War II (4). More recently, isolated teeth and bones (5) and the anterior half of an adult skull (6) have been discovered in the Kem Kem beds of eastern Morocco (Fig. 1A) and equivalent horizons in Algeria, but are insufficiently complete to estimate the size, proportions, and

functional adaptations of this species. Here we report the discovery of a partial skeleton of *S. aegyptiacus* from the middle of the Kem Kem sequence (Fig. 1B), which is probably Cenomanian in age (~97 million years ago) (7).

The subadult skeleton, here designated the neotype of *S. aegyptiacus* (8), preserves portions of the skull, axial column, pelvic girdle, and limbs. It was discovered in fluvial sandstone that has yielded remains of the sauropod *Rebbachisaurus* (9) and three other medium-to-large theropods (an abelisaurid, *Deltadromeus*, and *Carcharodontosaurus*) (7, 10). We regard two additional Kem Kem theropods, *Sigilmassasaurus brevicollis* and *S. maroccanus* (11, 12), to be referable to *S. aegyptiacus* (8).

The neotype skeleton and isolated bones referable to *S. aegyptiacus* were scanned with computed tomography, size-adjusted, and combined with a digital recreation of the original Egyptian fossils (Fig. 2A, red). Missing bones were extrapolated between known bones or estimated from those of other spinosaurids (6, 13, 14). The digi-

tal model of the adult skeleton of *Spinosaurus* (Fig. 2A), when printed and mounted, measures over 15 m in length, longer than *Tyrannosaurus* specimens (~12.5 m) (15).

A concentrated array of neurovascular foramina open on the anterior end of the snout and appear similar to foramina in crocodilians that house pressure receptors that detect water movement (8, 16) (Fig. 2B and fig. S6). The enlarged, procumbent, interlocking anterior teeth are well adapted for snaring fish (5, 6) (Fig. 2B and fig. S4). The fossa for the fleshy nostril is small and, unlike any other nonavian dinosaur, is retracted to a posterior position to inhibit the intake of water (Fig. 2C and figs. S4 and S6) (8).

Most cervical and dorsal centra are elongate compared to the sacral centra, resulting in a proportionately long neck and trunk (Figs. 2A and 3 and tables S1 and S2). The anteriormost dorsal centra, however, are proportionately short, exceptionally broad, and concavoconvex (Fig. 2D). These characteristic vertebrae, the affinity of which has been controversial (7, 11, 12), are referred here to *S. aegyptiacus*, based on their association with spinosaurid skeletons in Niger (8) and Egypt (2). The horizontal cervicodorsal hinge created by these broad centra would facilitate dorsoventral excursion of the neck and skull in the pursuit of prey underwater.

The distal two-thirds of the tail comprises vertebrae with relatively short centra, diminutive zygapophyses, and anteroposteriorly compressed neural spines (Fig. 2G). The affinity of these caudal elements has been uncertain (17), but comparisons with associated remains from Egypt (2) and more proximal caudals in the neotype (Fig. 2A) allow referral to *Spinosaurus*. Short centra and reduced neural arch articulations enhance lateral bending during tail propulsion in bony fish (18).

The forelimb has hypertrophied deltopectoral and olecranon processes for powerful flexion and extension (Fig. 2A). Elongate manual phalanges (Fig. 2H) and less recurved, manual unguals that

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are probably referable to *Spinosaurus* (11) and were possibly used in gaffing and slicing aquatic prey suggest that the manus is proportionately longer than in earlier spinosaurids (13, 14).

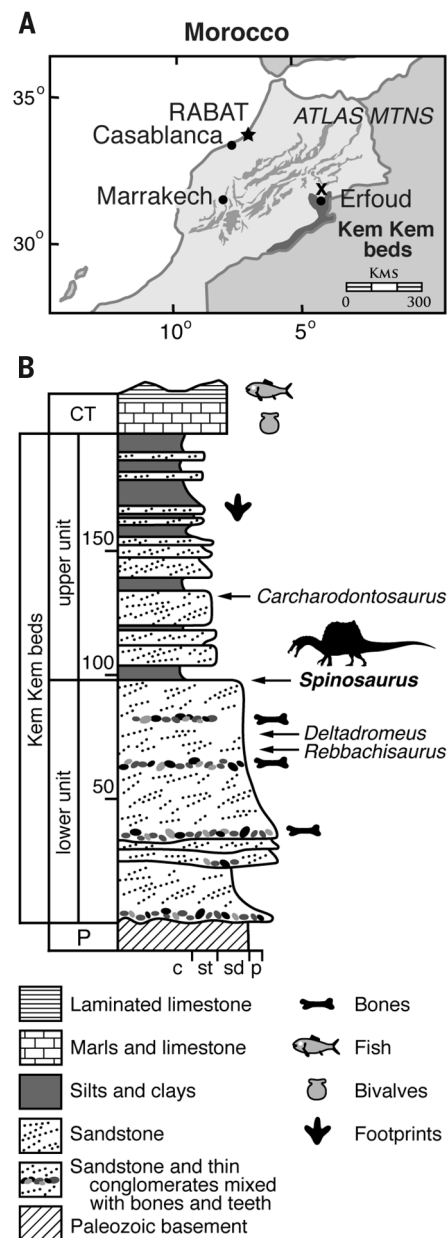
The pelvic girdle and hindlimb are considerably reduced in *Spinosaurus* (Fig. 2A). The surface area of the iliac blade is approximately one-half that in most other theropods (table S1), and the supraacetabular crest that supports the hindlimb

is low (Fig. 2F). Hindlimb length is just over 25% of body length (table S1). In a plot of forelimb, hindlimb, and body length (Fig. 3), *Spinosaurus* and other large theropods maintain fairly similar forelimb lengths. Relative hindlimb length, however, is noticeably less in the spinosaurid *Suchomimus* (25%) and especially in *Spinosaurus* (19%) than in other large tetanuran theropods.

Unlike other mid- or large-sized dinosaurs, the femur in *Spinosaurus* is substantially shorter than the tibia (Fig. 2, I and J, and table S1). In smaller-bodied bipedal dinosaurs, short femoral proportions indicate increased stride length and enhanced speed. In *Spinosaurus* this is clearly not the case, given the short hindlimb. The femur

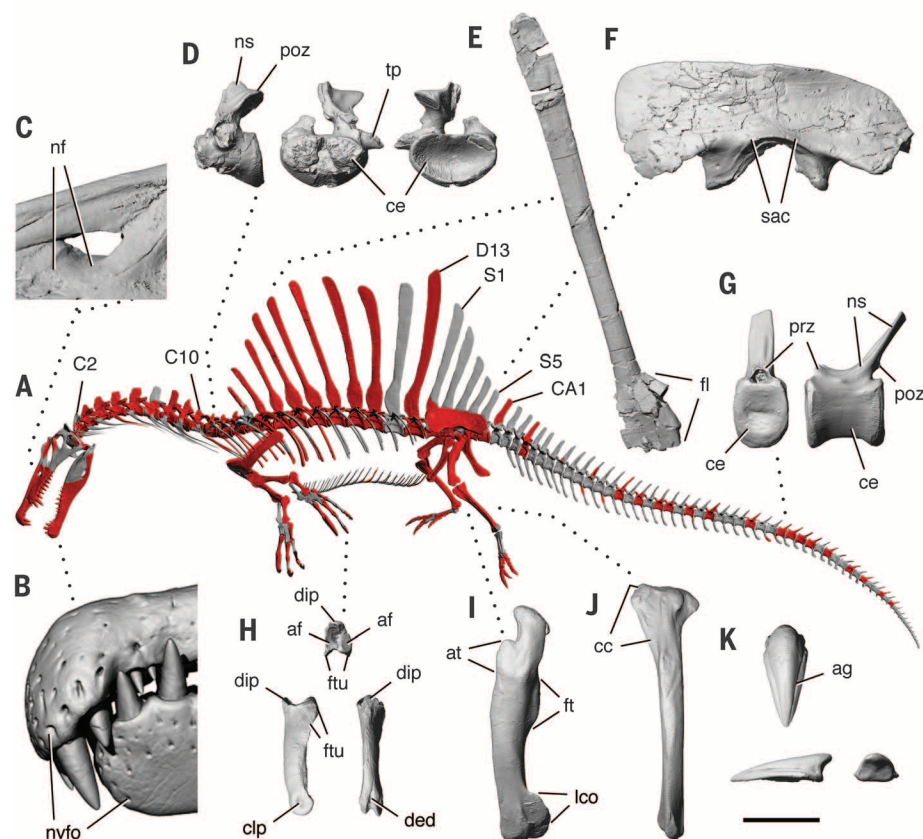
in *Spinosaurus* has an unusually robust attachment for the caudofemoral musculature, which is anchored along nearly one-third of the femoral shaft (Fig. 2I), suggesting powerful posterior flexion of the hindlimb. The articulation at the knee joint for vertical limb support, in contrast, is reduced. The distal condyles of the femur are narrow, and the cnemial crest of the tibia is only moderately expanded (Fig. 2, I and J). Together these features recall the shortened condition of the femur in early cetaceans (19, 20) and in extant semiaquatic mammals that use their hindlimbs in foot-propelled paddling (21).

Pedal digit I is unusually robust and long in *Spinosaurus*: Unlike *Allosaurus* or *Tyrannosaurus*,



**Fig. 1. Geographic location and stratigraphic position of the neotype skeleton of *S. aegyptiacus*.**

(A) Locality (X), situated 18 km northeast of Erfoud in southeastern Morocco. (B) Stratigraphic position at the base of the upper unit of the Kem Kem beds, with correlative positions of associated remains of contemporary dinosaurs. Abbreviations: c, clay; CT, Cenomanian-Turonian limestone; p, pebbles; P, Paleozoic; sd, sandstone; st, siltstone.

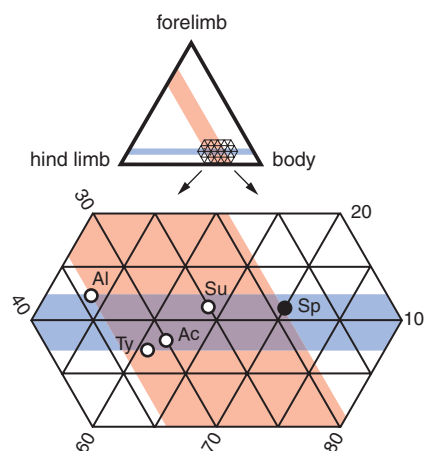


**Fig. 2. Semiaquatic skeletal adaptations in *S. aegyptiacus*.** (A) Skeletal reconstruction in swimming pose showing known bones (red) based on size-adjusted, computed tomographic scans of the neotype (FSAC-KK 11888), referred specimens, and drawings of original bones (1). (B) Rostral neurovascular foramina in lateral view (MSNM V4047) and a digital restoration of the holotypic lower jaw. (C) Narial fossa in lateral view (MSNM V4047). (D) Anterior dorsal vertebra (~D1) in lateral, anterior, and posterior views (UCRC PV601). (E) Dorsal neural spine (D8) in left lateral view (FSAC-KK 11888). (F) Left ilium in lateral view (FSAC-KK 11888). (G) Mid-caudal vertebra (~CA30, reversed) in anterior and left lateral views (UCRC PV5). (H) Right manual II-1 phalanx in proximal, lateral, and dorsal views (FSAC-KK 11888). (I) Left femur in lateral view (FSAC-KK 11888). (J) Right tibia (reversed) in lateral view (FSAC-KK 11888). (K) Right pedal digit III ungual in dorsal, lateral, and proximal views (FSAC-KK 11888). Abbreviations: af, articular facet; ag, attachment groove; at, anterior trochanter; C2, 10, cervical vertebra 2, 10; CA1, caudal vertebra 1; cc, cnemial crest; ce, centrum; clp, collateral ligament pit; D13, dorsal vertebra 13; ded, dorsal extensor depression; dip, dorsal intercondylar process; fl, flange; ft, fourth trochanter; ftu, flexor tubercle; lco, lateral condyle; nf, narial fossa; ns, neural spine; nvfo, neurovascular foramina; poz, postzygapophysis; prz, prezygapophysis; S1, 5, sacral vertebra 1, 5; sac, supraacetabular crest; tp, transverse process. Institutional abbreviations: FSAC, Faculté des Sciences Aïn Chock, Casablanca; MSNM, Museo di Storia Naturale di Milano; UCRC, University of Chicago Research Collection, Chicago. Scale bars, 10 cm in (B) to (D), (G), (H), and (K); and 20 cm in (E), (F), (I), and (J).



the first phalanx of digit I in *Spinosaurus* is the longest nonungual phalanx in the pes (fig. S1) and would have been in contact with the substrate in a stationary pose. The pedal unguals are proportionally large, long, low, and flat-bottomed (Fig. 2K and figs. S1 and S2), features that differ markedly from the deeper recurved unguals in other large theropods. The unguals in *Spinosaurus* are reminiscent of the flattened pedal unguals of shorebirds that do not perch (22). In addition, the toes of some shorebirds have fleshy lobes and interdigital webbing that enhance foot-propelled propulsion. The lengthened digit I and flattened pedal unguals in *Spinosaurus* suggest that the foot may have been adapted to traversing soft substrates or webbed for paddling.

Increases in bone mass and density are common skeletal modifications in terrestrial vertebrates transitioning to a semiaquatic existence (23). In *Spinosaurus*, this was achieved by enlarging midline display structures, eliminating open medullary cavities in the long bones, and increasing bone density. In subadult *Spinosaurus*, the dorsal neural spines are composed primarily of dense bone with only a narrow central zone of cancellous bone (Fig. 4D), and long bones have solid shafts (Fig. 4, A and C) with no development of the open medullary cavity that is present in other theropods, including early spinosaurids (Fig. 4B). Bone density within the long bones, in addition, is 30 to 40% greater in *Spinosaurus* than in other theropods (8).



**Fig. 3. Ternary morphospace plot comparing forelimb, hindlimb, and body length.** Forelimb (humerus + radius + metacarpal II), hindlimb (femur + tibia + metatarsal III), and body length (from snout tip to posterior extremity of pelvic girdle) are plotted as percentages of the sum of forelimb, hindlimb, and body lengths in *S. aegyptiacus* and other large tetanuran theropods (data from Table 1). Blue zone shows the range of forelimb length, from 7% (*Tyrannosaurus*) to 12% (*Allosaurus*). Hindlimb length (red zone) ranges from 34% (*Allosaurus*) to 19% (*Spinosaurus*). Abbreviations: Ac, *Acrocanthosaurus*; Al, *Allosaurus*; Sp, *Spinosaurus*; Su, *Suchomimus*; Ty, *Tyrannosaurus*.

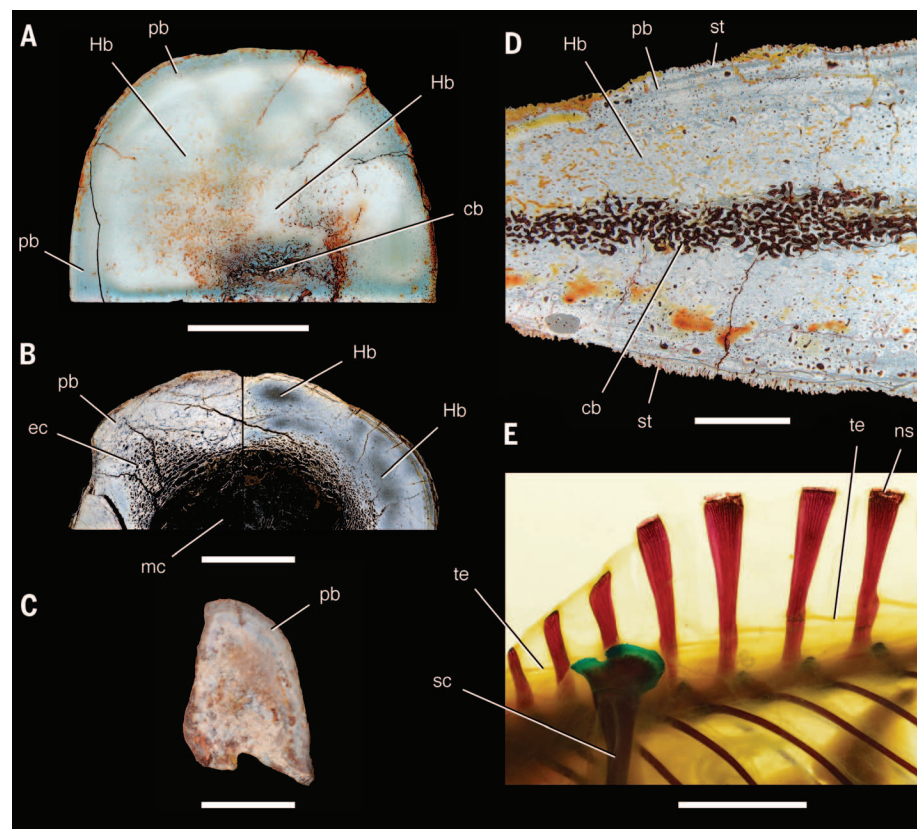
We estimated a center-of-body mass for a flesh rendering of *Spinosaurus* created over the digital skeleton (8). Center-of-mass estimates for several theropods have been expressed as a percentage of femoral length measured anteriorly from the hip joint (24). The center of mass in a biped must be located over the middle one-third of the pes to generate a plausible mid-stance pose (25). In our flesh rendering of *Spinosaurus*, the center of body mass is positioned in front of both the hip and knee joints at a distance greater than femur length (fig. S3), suggesting that forelimb support was required during terrestrial locomotion. *Spinosaurus* appears to have been poorly adapted to bipedal terrestrial locomotion. The forward position of the center of mass within the ribcage may have enhanced balance during foot-propelled locomotion in water.

These adaptations suggest that *Spinosaurus* was primarily a piscivore, subsisting on sharks, sawfish, coelacanth, lungfish, and actinopterygians that were common in the Kem Kem river system (5, 7, II). A long narrow skull and powerful forelimbs are also present in earlier spinosaurids, which

like *Spinosaurus* (26) have been interpreted as predominantly piscivorous (13, 14, 27, 28).

The locomotor adaptations outlined above, however, mark a profound departure in form and function from early spinosaurids. Prominent among these are the reduced pelvic girdle; short hindlimb; short femur; and long, low, flat-bottomed pedal unguals, all of which can be verified in the second partial skeleton described by Stromer as “*Spinosaurus B*” (2, 8). We note here that *Spinosaurus* must have been an obligate quadruped on land, the first discovered among theropod dinosaurs, given the usual horizontal sacroiliac joint and the anterior location of the estimated center of body mass (8). *Baryonyx* was interpreted as a facultative quadruped, based on its long skull and neck and robust humerus (27), but this was not confirmed by the discovery of more complete hindlimb remains of the related *Suchomimus* (13).

In *Spinosaurus* we infer foot-powered paddling from the relatively short femur with hypertrophied flexor attachment and strong pedal digit I, as occurs in semiaquatic mammals such as early cetaceans (19–21). Low, flat-bottomed pedal unguals are coincident with digital lobes or webbing in



**Fig. 4. Bone microstructure and dorsal spine form.** (A) Mid-shaft thin section of the right femur of *S. aegyptiacus* (FSAC-KK 11888). (B) Mid-shaft thin section of the right femur of *Suchomimus tenerensis* (MNN GAD608). (C) Cross-sectional view of right manual II-1 phalanx of *S. aegyptiacus* (FSAC-KK 11888). (D) Thin section of a dorsal neural spine (distal section) in *S. aegyptiacus* (FSAC-KK 11888). (E) Dorsal vertebrae with tall neural spines and spinal tendons in a cleared and stained specimen of *Trioceros* (*Chamaeleo*) *cristatus* (FMNH 19886). Abbreviations: cb, cancellous bone; ec, erosional cavities; Hb, Haversian bone; mc, medullary cavity; ns, neural spine; pb, primary bone; sc, scapula; st, striae; te, tendon of multisegment spinal muscle. Institutional abbreviations: FMNH, Field Museum of Natural History. Scale bars, 2 cm in (A) and (C), 3 cm in (B), 5 mm in (D), and 1 cm in (E).

shore birds (22), and interdigital webbing has been reported in theropod dinosaurs (29).

Reduction of the pelvic girdle and hindlimb and the concomitant enhancement of axial-powered locomotion are common among semiaquatic vertebrates. The flexibility of the tail and the form of the neural spines in *Spinosaurus* suggest tail-assisted swimming. Like extinct and extant semiaquatic reptiles, *Spinosaurus* used lateral undulation of the tail, in contrast to the vertical axial undulation adopted repeatedly by semiaquatic mammals (20, 21).

The dorsal "sail" in *Spinosaurus*, the tallest axial structure documented among dinosaurs, has been argued to be a thermoregulatory surface, a muscle- or fat-lined hump (30), or a display structure. Stromer (1) drew an analogy to the skin-covered neural spines of the crested chameleon, *Trioceros cristatus* (Fig. 4E). As in *T. cristatus*, the sail of *Spinosaurus* is centered over the trunk (Fig. 2A). The shape and positioning of the spine are also similar, and the base of the neural spine is expanded anteroposteriorly, with edges marked by ligament scars (Fig. 2E). In *Trioceros*, a tendon of multisegmental axial musculature attaches to the expanded base of the neural spine (Fig. 4E). The upper portion of the spine has sharp anterior and posterior edges, is marked by fine vertical striae (Figs. 2E and 4D), and is spaced away from adjacent spines, unlike the broader, contiguous, paddle-shaped dorsal spines of other spinosaurids (13). The striated surface, sharp edges, and dense, poorly vascularized internal bone of the spines suggest that they were wrapped snugly in skin and functioned as a display structure that would have remained visible while swimming.

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## SUPPLEMENTARY MATERIALS

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## NEUROSCIENCE

# A critical time window for dopamine actions on the structural plasticity of dendritic spines

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Animal behaviors are reinforced by subsequent rewards following within a narrow time window. Such reward signals are primarily coded by dopamine, which modulates the synaptic connections of medium spiny neurons in the striatum. The mechanisms of the narrow timing detection, however, remain unknown. Here, we optically stimulated dopaminergic and glutamatergic inputs separately and found that dopamine promoted spine enlargement only during a narrow time window (0.3 to 2 seconds) after the glutamatergic inputs. The temporal contingency was detected by rapid regulation of adenosine 3',5'-cyclic monophosphate in thin distal dendrites, in which protein-kinase A was activated only within the time window because of a high phosphodiesterase activity. Thus, we describe a molecular basis of reinforcement plasticity at the level of single dendritic spines.

**A**nimal behaviors are reinforced only when rewarded shortly after a motor or sensory event (1, 2). The neocortex, hippocampus, and amygdala process the sensorimotor signals and send glutamatergic synaptic output to the striatum (3), where connections can be modified by Hebbian learning mechanisms,

such as spike-timing-dependent plasticity (STDP) (4). Animals learn to associate the sensorimotor signals with subsequent rewards through reinforcement of the neuronal circuits involving dopamine (5–7). Despite its importance, this narrow timing detection has never been demonstrated at the cellular level and might be ascribed to neural network properties (6, 8).

Dendritic spine morphology is correlated with spine function (9), and dendritic spines enlarge during long-term potentiation in the cortices (10–12). We examined the effects of dopamine on the structural plasticity in striatal medium spiny neurons (MSNs). Results show that dopamine affected spine structural plasticity in a narrow time window consistent with behavioral conditioning (5). Functional imaging revealed the molecular interrelationships between the reinforcement and Hebbian plasticity.

We investigated dopamine actions on glutamatergic synapses on MSNs using optogenetics and

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