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How Affordances Associated with a Distractor Object Can Cause Compatibility

Effects: A Study with the Computational Model TRoPICALS

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Abstract

Seeing an object activates both vision and action codes in the brain. The primary evidence for this view is

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given by compatibility effect experiments that show that an object's affordances can facilitate or interfere with the execution of an action (e.g. grasping) even when the viewer has no intention of interacting with the object (e.g. handling it). TRoPICALS is a computational embodied neuroscience model which has been previously proposed as a general framework to account for compatibility effects. The model has a flexible architecture which allows the reproduction and interpretation of several different compatibility effects and the generation of predictions testable in the lab. Importantly, TRoPICALS supplies an hypothesis about the brain mechanisms underlying compatibility effects, in particular that the excitatory top-down prefrontal cortex bias based on the experimental task, and its agreement or disagreement with the affordances of objects, play a key role to explain such phenomena. Ellis, Tucker, Symes, and Vainio (2007) have investigated what happens when a visual target object has to be attended in the presence of distractor object. In this experiment the authors measured the participants' reaction times to produce the responses requested by the experiment (to classify as either "round" or "square", by producing a precision or a power grip, a target 3D object presented on a computer screen) and studied how they were influenced by the congruence or incongruence of the distractor size with the requested responses. The results confirmed the target-related compatibility effects found in previous experiments without the distractor, and also showed an unexpected interesting effect of the distractor: responding to a target with a grip *compatible* with the action afforded by the distractor produced *slower* reaction time in comparison to the incompatible case. The authors interpreted these results proposing that the inhibition of the action elicited by the distractor interfered with the execution of similar actions in comparison to different actions. This work presents a new version of TRoPICALS that reproduces these results and allows explaining them on the basis of the detailed neural mechanisms that could underlie the interference/facilitation effects caused by the perception of the distractor contextually with the target. This explanation is based on a novel idea according to which the prefrontal cortex might play a double role in its top-down guidance of action selection: (a) producing a positive bias directed to trigger the actions requested by the experimental task; (b) producing a negative bias directed to inhibit the action evoked by the distractor. The model also provides testable predictions related to the possible consequences on compatibilities effects of the target and distractor in Parkinsonian patients with damages of volitional circuits.

Paper size: 10 000 words (including references and abstract). Reduce this value further (by 350 words) for each

Figure and Table

Intro: 1 000 words

Introduction

A classical approach to human cognition proposes that the processes related to perception, high-level cognition (such as decision making), and action, take place in successive and relatively independent stages (e.g., Sternberg, 1969). In the last years, this approach has been challenged by the view for which the whole mind and the underlying brain mechanisms are strongly shaped by the need to serve action (Clark, 1996; Varela, Thompson, & Rosch, 1999). In the development of action-based theories of cognition the concept of *affordance* (Gibson, 1979), for which objects and the environment around us are seen by organisms in terms of the opportunity for actions they offer, has played an influential role. Indeed, behavioural and brain imaging experiments are now showing that the simple sight of objects tends to elicit internal motor representations, suggesting that for organisms the very notion of object has fundamental action components (Jeannerod, 1994; Arbib, 1997; Rizzolatti, Fogassi, & Gallese, 1997).

Cognitive psychologists have developed an experimental paradigm to investigate these issues from a behavioral perspective: the *affordance compatibility paradigm*. In a typical experiment (Tucker & Ellis, 2001; Tucker & Ellis, 2004), the participants of the test are requested to respond to some objects, for example to classify them as *natural* or *artifact*, by producing either a precision or power grip action on a custom joystick. Evidence obtained with RTs shows that the affordance for a precision or power grip respectively elicited by small or large objects tends to favour compatible categorisation responses and interfere with incompatible one, even if size is not relevant for the task.

In a previous work on this phenomena we proposed a *Computational Embodied Neuroscience (CEN)* model

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The success of TRoPICALS in explaining the target phenomena is largely due to its embodied nature. Indeed, although the sensorimotor loop of the model was not strictly closed due to the nature of the target experiments (the fact that action strongly changes the system's input is a fundamental aspect of embodiment, cf. Nolfi & Floreano, 2000 and Nolfi, 2009) some “embodied features” of TRoPICALS revealed fundamental to explain compatibility effects. For example, the use of a realistic two-dimensional simulated retina generated the need to have the two dorsal and ventral visual neural pathways to support affordance processing; the opportunity to consider both object affordances and agent's goals generated the synergies and conflicts underlying compatibility effects; the need to integrate information to decide between different actions led to have neural competitions that explained the reaction times found in empirical experiments.

This work accomplishes another important step in understanding the grounding of cognition in action. The world is full of objects and features (henceforth referred to as *distractors*), most of which are irrelevant to the agent's purposes. If the internal representation of objects involve elements of the affordances they elicit, then the active suppression of the actions related to non-target distractors should interfere with the execution of other actions that share with them common features or parameters. This is indeed what has been observed in the experiment of Ellis, Tucker, Symes, and Vainio (2007). In this case, the view of a distractor irrelevant for the execution of a categorisation task (the one of Tucker & Ellis, 2001 and 2004, reviewed above), led to *slow down* response RTs in case of *compatibility* between the distractor size and the requested precision/power response, and to speed them up in the opposite case.

The main aim of this paper is to investigate which is the role played by *excitatory and inhibitory mechanisms on compatibility effects*. To this purpose, the article presents an extended version of TRoPICALS that reproduces the main results of Ellis, Tucker, Symes, and Vainio (2007) (both those related to the target compatibility effects and the

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distractor “opposite” compatibility effects) and allows explaining them on the basis of the neural mechanisms that could underlie the interference/facilitation effects caused by the contextual perception of a distractor and a target object. The extension is based on the idea for which PFC might play a *double* role in its top-down guidance of action selection (Knight, Staines, Swick, & Chao, 1999): (a) by producing a positive bias that facilitates the triggering of the actions requested by target objects; (b) by producing a negative bias that inhibits neural representations at the basis of the activation of affordances related to distractors.

Key empirical evidences that might give important insights on *excitatory and inhibitory mechanisms on compatibility effects* come from the research on Parkinson Disease (PD) patients (Lang & Lozano, 1998; Redgrave et al., 2010). PD involves both damages of excitatory/inhibitory mechanisms underlying action selection and execution and a difficulty in starting volitional movements. The difficulties in selecting and executing actions is caused by the loss of dopaminergic cells of the nigrostriatal pathway injecting dopamine into the Basal Ganglia (BG), in particular into the portions of the latter that form loops with the premotor (PMC) and motor cortex (MC; the loops formed with PMC/MC play a key role in action learning and selection). PD patients also have difficulties in starting voluntary movements. This is attributed to the underactivation of the supplementary motor area (pre-SMA), again caused by dopaminergic deficits in this case involving the portions of BG that form loops with this cortical area (Jahanshahi et al., 1995). Indeed, the pre-SMA bridges the PFC (where goals and needs are represented) to the PMC/MC (responsible for action preparation and execution) and so plays a crucial role in generating actions with an internal origin (Nachev, Kennard, & Husain, 2008; Haggard, 2008). In contrast with this difficulty, PD patients are particularly susceptible to react to affordances (Galpin, Tipper, Dick, & Poliakoff, 2010). Much evidence shows that such sensitivity to externally evoked actions can help the movements of PD patients by compensating the effects of the underactivation of the pre-SMA (e.g., see Galpin, Tipper, Dick, & Poliakoff, 2010; Oguro, Ward, Bracewell, Hindle, & Rafal, 2009). Given that the brain damages of PD patients are mostly known, it is possible to perform similar damages to the model, to advance empirical predictions on the possible outcome of compatibility tests on PD patients, and to test them in empirical experiments.

The target psychological experiment and its simulation

In one of the experiment reported by Ellis et al (2007) the participants were asked to select the target object (blue) from a two-object scene (presented on a computer monitor) including a distractor object (red). The experiments used four objects with different shapes: two large objects (cylinder and parallelepiped) and two small objects (sphere and cube). The participants were requested to produce a response to the target object by mimicking a precision grip response on a customised joystick if the objects was curved (small sphere or large cylinder) or by mimicking a precision grip response if it was straight (small cube or large parallelepiped). Each scene never presented a target and a distractor from the same

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The results confirmed the target-related compatibility effect found in Tucker and Ellis (2001), that is RTs were faster when the kind of response used to classify and the affordances evoked by the objects were congruent. Importantly, the results also showed that the performance was strongly affected by the action properties of the distractor object. In particular, responding to a target with a grip type that was compatible with the action properties of the distractor object produced a decrement in performance relative to the incompatible cases. The authors interpreted these results arguing that selecting an object to act upon (the target) requires inhibition of the action associated with a non-selected object (the distractor).

The simulations aimed at reproducing this experiment, simplifying secondary aspects of it. The simulated participant could see eight different objects drawn from the original experimental set: four target blue objects (small sphere, large cylinder, small cube, large block), and four distractor red objects with the same shape of the target objects. The small objects could be graspable with a precision grip, whereas the large objects with a power grip. In the simulated experiments, the nervous system of 10 participants was simulated by using 10 different neural networks having different randomly-drawn initial connection weights. After this training, the RTs of the participants were recorded after blocking all learning processes.

Differently from what happened in the laboratory, before undergoing the experiment the simulated participant first learned to associate a suitable kind of grip (e.g., a precision one) to each object (e.g., a small sphere). This learning procedure was used to mimic what happens in the life of real participants when they learn to suitably respond to affordances of objects. Note how this is an essential element of the explanation of the compatibility effects presented here as such explanation relies on the hypothesis of the reactivation of internal representations of affordances acquired *before* the psychological experiment.

Methods

The body of the simulated participants

The neural network model controlled the body of a 3D simulated participant endowed with a visual system, a human-like 3-segments/4-degrees of freedom (DOFs) arm, and a 21-segments/19-DOFs hand (Figure 1 (a)). The simulated participant's arm and hand had the same parameters of the humanoid robot iCub (<http://www.icub.org>). The visual system of the participant was formed by a simulated "eye" (a 630 × 630 pixel RGB camera with a 120° pan and a 120° tilt angle, see figure 1a). This was mounted 25cm above the shoulder, leaned forward 10cm, and looked down at the

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working plane where the arm performed actions. The eye was controlled by a hardwired “focussing reflex” that led it to foveate the barycentre of the objects. In particular, each of the desired pan and tilt angles of the eye was computed as follows:

$$a[t+\Delta t] = a[t] + 120 \frac{c - 315}{630} \Delta t \quad (1)$$

where $a[t]$ is the pan angle to be computed at time t , 315 is the centre of one dimension of the image (in pixels), 630 is the image size (in pixels), c is the weighted average of the x (or y for tilt) position within the retina (ranging in $[0, 630]$) of the pixels having the desired colour (the average has weights equal to the activation of the pixels), and 120 is the movement range of the camera in each dimension (in degrees). The reflex is in line with the current neuroscientific literature suggesting that primates tend to foveate the target objects with which they interact and that their brain tends to exploit gaze centred reference frames for sensorimotor coordination (Shadmehr & Wise, 2005).

During the experiments the system was exposed to a scene showing two objects: a target object and a distractor. The target was chosen among four different blue objects: two large objects (cylinder: radius 34 mm, length 70 mm; parallelepiped base side 60 mm, length 80 mm), and two small objects (sphere: radius 15 mm; cube: side 25 mm); the distractor was chosen among objects which could have the same size and shape of the target objects, but with a different colour (red instead of blue).

To simplify the analysis of results, the images sent to the system were caused only by the target and distractor objects and not by the hand: this amounts to assuming that the system could filter out the hand on the basis of a suitable object-based attention mechanism not explicitly simulated here (Logan, 1996; Roelfsema, Lamme, & Spekreijse, 1998). In this respect, it is also important to consider that seeing an object is sufficient to activate the representations of its affordances in the parietal area (AIP) and pre-activate motor neurons in pre-motor area (PMCI) (in particular, “canonical neurons”; Rizzolatti & Craighero, 2004).

The model controlled only 2-DOFs of the hand: one for the thumb, whose DOFs are all controlled proportionally to a first command issued by the model, and one for the four same-sized fingers, controlled as a whole “virtual finger” (cf. Arbib, 2002) proportionally to a second command. The DOFs of the wrist and arm were kept still as requested by the tasks of the target experiment.

The activation of the grasping output map of the model (PMCI in figure 1b) encoded the desired hand posture which was used to set the hand and arm “muscle models” in terms of “equilibrium points” (Feldman, 1986). In particular, similarly to what was done in Berthier, Rosenstein, and Barto (2005), single muscle models were simulated as simple Proportional Derivative controllers (PDs) which capture the main elastic and damping properties of muscles. The equation of a PD muscle controller is as follows (Sciavicco & Siciliano, 1996):

$$T = K_P \Phi + K_D \dot{\Phi} \quad (2)$$

where T is the vector of muscle torques applied to the joints, K_P is a diagonal matrix with elements equal to 300, Φ is the difference vector between the desired angular positions and the current angular positions of joints, K_D is a diagonal matrix with elements equal to 10, and $\dot{\Phi}$ is the vector of current angular speed joints. This muscle model implies that the difference between the desired joint angles set by the system and the actual joint angles is used to set a proportional torque which diminishes it. In addition to this, the muscle model also generated a torque opposite to the movement and proportional to the joint angular speed which resulted in a dumping effect which increased the arm stability. The action of the PDs was also assumed to be integrated by a gravity compensation mechanism here implemented by simply ignoring the effects of gravity on the arm and hand.

Model features: architecture, functioning, and learning

In this paper we propose a modified version of the TRoPICALS model (Caligiore, Borghi, Parisi, & Baldassarre, 2010; preliminary ideas about this modified version of the model were discussed in Caligiore et al., 2011), which reproduces the results of Ellis, Tucker, Symes, and Vainio (2007) and allows explaining them on the basis of the neural mechanisms that could underlie the interference/facilitation effects caused by the contextual perception of a distractor and a target object. In the enhanced version of TRoPICALS proposed here PFC plays a double role in its top-down guidance of action selection (Knight, Staines, Swick, & Chao, 1999) producing both a positive bias that facilitates the triggering of the actions requested by target objects and a negative bias that inhibits the neural representations encoding the affordances related to distractors.

Architecture

Figure 1b illustrates the architecture of the modified TRoPICALS model used here. The architecture of the model is formed by five components each corresponding to a different brain cortical area: the visual cortex (VC; three RGB maps of 21×63 neurons), the anterior intraparietal area (AIP; one map of 21×63 neurons), the lateral premotor cortex (PMC; one map of 21×63 neurons), the ventral occipito-temporal cortex (VOT; one map of 21×21 neurons), and the prefrontal cortex (PFC; one map of 21×21 neurons). The choice of the components of the architecture of the model is broadly in line with brain imaging evidences which shows that portions of parietal, premotor, temporal, and frontal cortex of humans engaged in compatibility effect experiments (Grèzes, Tucker, Armony, Ellis, & Passingham, 2003). The components of the model, their functioning, and the biological reasons for the assumptions related to them are now presented in detail.

Insert Figure 1 about here

Visual cortex (VC)

In brains of monkeys (Van Essen et al., 2001) and humans (Van Essen et al., 2001, Grill-Spector & Malach, 2004), early stages of visual cortex (VC) are hierarchically organised. This hierarchy performs a processing of visual information which leads to extract increasingly abstract information from visual images, from simple edge detection (Hubel, 1988) to complex feature recognition (Vinberg & Grill-Spector, 2008). Information elaborated in VC is important for both object recognition processes taking place in the ventral pathway and the sensorimotor transformations taking place in parietal cortex and needed to guide action (see below).

Differently than the early version of TRoPICALS (Caligiore, Borghi, Parisi, & Baldassarre, 2010), VC processes target and distractor at the same time. As before, VC is formed by three maps encoding three colours of the image (Red, Green, and Blue). However now VC has a central region representing the fovea and its surroundings, and two lateral regions representing the peripheral left and right parts of the retina. The central region is always activated by the target object whereas either one of the peripheral regions is activated by the distractor (the model assumes that the eye always foveates the target on the basis of the “focussing reflex” illustrated above). The neurons of central region have an activation which ranges in $[0, 1]$ whereas those of the peripheral regions have an activation which ranges in $[0, 0.4]$ to simulate the lower density of receptors of the peripheral areas of the retina. The three colour maps encode the information about shape and colour of the seen object obtained through three distinct Sobel filters (Sobel & Feldman, 1968) applied to the three colour maps. These processes abstract the edge detection processes performed by the retina and by the succeeding early stages of visual cortex in humans.

Anterior intraparietal area (AIP)

In monkeys parietal cortex (PC) the anterior intraparietal area (AIP) encodes information about features of objects which are important to guide manipulation, for example shape, orientation, 3D aspects (Rizzolatti, Luppino, & Matelli, 1998; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000). AIP neurons also discharge during goal directed actions performed with the hand and mouth (e.g., grasping, holding, and manipulation). AIP receives important connections from PFC (Borra et al., 2008; Baumann, Fluet, & Scherberger, 2009), so possibly positioning it at a high level in the hierarchy of action selection. On the basis of this evidence, many authors claim that AIP is one of the most important

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brain areas encoding object affordances (Fagg & Arbib, 1998; Oztop, Bradley, & Arbib, 2004). The human homologue of the monkey AIP might equally be the anterior intraparietal (AIP) area which is activated by the manipulation of objects and the view of graspable objects (Culham & Kanwisher; Simon, Mangin, Cohen, Hihan, Dehaene, 2002).

In the model, AIP encodes information about object shape (the representation of the “shape” of objects used here should be considered as a “proxy” of the various object properties encoded in AIP). In particular, the neurons forming this map are activated with the average activation of the topologically correspondent RGB edge-encoding neurons of VC. This implies that the model assumes that when the system processes two objects located at different positions at the same time (e.g.m target and distractor) such processing activates different areas of AIP. This amounts to assuming some spatial sensitivity of AIP (Behrmann, Geng, & Shomstein, 2004).

Another assumption of the model related to AIP is that in the model the PFC is only connected to the PMC and not to the AIP. The PFC-PMC pathway should be considered as a proxy of the whole influence that PFC exerts on both PMC and AIP: the two pathways were not explicitly represented in the model as this was not necessary for the goals of this work. A last assumption on the AIP relates to the fact that the activation process described above causes large objects to activate a much larger number of neurons with respect to small ones, whereas empirical evidence shows that the opposite happens in real brains (Ehrsson et al., 2000). This is likely due to the fact that the interaction with small objects requires a more sophisticated and detailed control of fingers. Although the level of abstraction of the model did not allow representing these differences, we used a coefficient s to scale the activation of AIP neurons based on the size of objects (s was set to 1 for large objects and to 3.2 for small objects and was used to multiply the activity of all neurons of AIP). This assumption, that reproduced the data on the activation of AIP only at *phenomenon* level, was sufficient to avoid possibly undesired distortions on reaction times caused by different activations of AIP by large/small objects.

Premotor cortex, lateral division (PMCl)

In monkeys, the PMC area F5 has been extensively studied as it seems to encode a rich repertoire of actions such as precision, power and side grasps not only when these are performed but also when they are observed (Rizzolatti, Luppino, & Matelli, 1998; Rizzolatti & Craighero, 2004). The human homologue of the monkey F5 might be area 44 in the lateral premotor cortex, here referred to as PMCl (Rizzolatti et al, 1998).

In the model, the neurons of PMCl encode the output of the system in terms of desired hand fingers' angles: these angles, mapped onto the 2 dimensions of the map, are “read out” as a weighted average of the neurons' position in the map with weights corresponding to the neurons' activation (“population code hypothesis”, Pouget, Dayan, & Zemel, 2000). The PMCl supports the selection of postures on the basis of a dynamic competition involving the leaky neurons

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which form it. These neurons have short-range lateral excitatory connections and long-range lateral inhibitory connections (Erlhagen & Schöner, 2002). When input signals from AIP and PFC activate neurons of PMCI, these tend to accumulate activation and to form clusters (due to the lateral excitatory connections) and, at the same time, to suppress other clusters (via lateral inhibitory connections). This dynamic process continues until a cluster succeeds to suppress all other clusters, overcomes a threshold and triggers the hand movement based on the reading out of the map described above. Mathematically, each PMCI leaky neuron activates as follows:

$$\begin{aligned}
 s_j[t] &= \sum_{i=1}^N \overbrace{w_{PMCI \rightarrow PMCI}}^{Inner} a_{PMCI}[t] \times \sum_{i=1}^N \overbrace{w_{PC \rightarrow PMCI}}^{Dorsalstream} a_{PC}[t] \times \sum_{i=1}^N \overbrace{w_{PFC \rightarrow PMCI}}^{Ventralstream} a_{PFC}[t] \\
 u_j[t+\Delta t] &= \frac{\Delta t}{\tau} s_j[t] \\
 a_j[t+\Delta t] &= [\tanh[u_j[t+\Delta t]]]^+
 \end{aligned} \tag{3}$$

where $s_j[t]$, $u_j[t]$ and $a_j[t]$ are respectively the input signal, the activation potential, and the activation of neuron j at time t , Δt is the integration time step (Δt was set to 0.01 sec, which implies that 100 steps of simulation correspond to 1 sec of real time), τ is a time constant (τ was set to 0.5 sec), $\tanh[\cdot]$ is the hyperbolic tangent function, and $[\cdot]^+$ is the identity function returning 0 for negative values. The *Inner* component of the input signal accounts for signals received from lateral PMC connections having hardwired connection weights $w_{(PMC \rightarrow PMC)}$. These weights, excitatory for connections between neighbouring neurons and inhibitory for connections between distant neurons, are set to fixed values on the basis of a Gaussian function and an inhibition term as follows:

$$w_{(PMC \rightarrow PMC)ji} = \alpha \exp \left[-\frac{\|v_j - v_i\|^2}{2\sigma^2} \right] - I \tag{4}$$

where $w_{(PMC \rightarrow PMC)ji}$ is the weight between two neurons i and j of the map, $\|v_j - v_i\|$ is the Euclidean distance between the two neurons in the map “neural space” (the measure unit being the distance between two neighbouring neurons), α is the height of the Gaussian function (α was set to 1.2), σ is its width (σ was set to 0.6), and I is the inhibition term (I was set to 0.4). The *Dorsal stream* component of the input signal accounts for the signals received from PC neurons through connections having weights $w_{(PC \rightarrow PMC)}$. Finally, the component *Ventral stream* accounts for the signals received from PFC neurons through connections having weights $w_{(PFC \rightarrow PMC)}$. Note that the weights $w_{(PFC \rightarrow PMC)}$ were kept within the interval $[0, 0.3]$ and the weights $w_{(PC \rightarrow PMC)}$ within the interval $[0, 0.1]$ as PFC signals need to overwhelm affordance-related signals when necessary (Miller & Cohen, 2001).

Equation (3) represents an abstract way to simulate the competition based on reciprocal inhibition of competing clusters which might actually take place within whole systems formed by basal ganglia/cortical loops

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Within the model, reaction times correspond to the time requested by at least one neuron of the winner cluster of PMC to reach the action-triggering threshold (Erlhagen & Schöner, 2002; the threshold value was set to 0.7). An important caveat on the RTs produced by the model is that they rely upon various coefficients which could not be set to realistic values drawn from the properties of real neurons due to the relatively high abstraction level of the neurons of the model (firing rate neurons; cf. Dayan & Abbott, 2001). For this reason, the model was intended to reproduce only the pattern of qualitative results of the target experiments, but not their quantitative levels (e.g., in relation to the specific RTs exhibited by the real participants, cf. Erlhagen & Schöner, 2002). A sensitivity analysis on the qualitative effects that some key parameters of the model produce on RTs is shown in Caligiore, Borghi, Parisi, and Baldassarre (2010).

Ventral occipito-temporal cortex (VOT)

In monkey brain, the inferior temporal cortex (IT) is located at the highest levels of the ventral visual pathway and plays an essential role in visual object recognition (Van Essen et al., 2001; Logothetis, Pauls, & Poggio, 1995). In humans, various areas within the ventral visual pathway have an activation which responds to highly abstract patterns (e.g., faces, places) and is rather invariant with respect to aspects of images such as location, orientation, and luminance (Grill-Spector & Malach, 2004; Vinberg & Grill-Spector, 2008). Among these areas, the ventral occipito-temporal cortex (VOT) seems to play a key role in object recognition.

In the model, VOT is represented by one self-organising map (“SOM”; Kohonen, 1997). The map receives all-to-all connections from the three RGB maps of the VC. An important assumption of the model is that when the VC-VOT connection weights corresponding to one of the three regions of VC are updated (see below), the also the corresponding weights of the other two regions are updated in the same way (but those of the peripheral regions are updated with a learning rate that is 40% of that used for the fovea region connections to reflect their lower density of receptors and a partial sensitivity to spatial locations of objects, cf. Grill-Spector, 2008). This technique, well known in the neural modelling field, is used to assure a spatially-invariant representation of objects within the VOT typical of high-level visual processing stages of brain. Note that this assumption also allows the VOT to represent two or more different objects at the same time when these are perceived contextually.

In the model each unit of the SOM map is activated as follows:

$$a_j = \exp \left[- \frac{\|a_{VC} - w_{VC \rightarrow VOT_j}\|^2}{2\sigma^2} \right] \quad (5)$$

where a_j is the activation of VOT neuron j , a_{VC} is the vector of activations of VC neurons, $w_{(VC \rightarrow VOT)_i}$ is the vector of the

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connection weights linking VC neurons to VOT neuron j , σ is the size of the Gaussian function used to compute the activation (σ was set to 0.55). The Kohonen network tends to form weights such that for any given input pattern the activation function causes a hill-shaped activation of a cluster of neurons of the map whereas the other neurons remain silent. Moreover, similar input patterns tend to activate similar clusters of neurons whereas different input patterns tend to activate non-overlapping clusters.

Prefrontal cortex (PFC)

The prefrontal cortex (PFC) is a crucial source of top-down biasing which instructs and informs the neural competitions between potential actions that compete for expression in behaviour (Miller & Cohen, 2001; Cisek, 2007). The sensory system of primates provides detailed information about the external world and as a result of this their motor system can acquire a large repertoire of actions. This introduces a great potential for flexibility but also for interference. To effectively cope with the multitude of possible actions to perform, the brain has acquired mechanisms that coordinate low-level sensory and motor processes on the basis of internal motivations, goals, and external context (Fuster, 1997; Fuster, 2001). The PFC plays a key role in these processes especially when “top-down” control based on motivations and goals is needed (Fuster, 2001; Miller & Cohen, 2001).

PFC also exhibits a high degree of plasticity. At the neural level, the mechanisms that underlie this plasticity could involve the modification of synapses, possibly with the assistance of rapid learning processes taking place in the hippocampus (Rolls & Treves, 1998). PFC can perform these functions in a more flexible way than lower sensorimotor processes, for example it can learn behavioural sequences “on the fly” (in humans it can do this on the basis of reciprocal interconnections with language areas, Pulvermüller, 2005) and it can store context in working memory so that it can suitably switch the “rules” of the produced behaviour in correspondence to relevant events (Hazy, Frank, & O’Reilly, 2007).

This higher flexibility and context sensitivity of PFC allows it to strongly bias action selection when the multimodal richness of information and external/internal context requires to suitably modulate action instead of acting on the basis of habits and automatic tendencies (e.g., see also the literature on goal-driven behaviour, e.g. Balleine & Dickinson, 1998, and Daw, Niv, & Dayan, 2005).

In the previous version of TRoPICALS, the PFC received information not only about the objects but also about the context (e.g., laboratory experiment vs. ecological conditions), and could form different representations of the situation on such basis (based on a Kohonen network). This is in line with the fact that the PFC collects information about the external world, current context, and internal needs of the organisms in order to select the overall goals of the system (Deco & Rolls, 2003). To solve the experimental task considered here, the PFC needed only the information from the visual seen (target and distractor), so the PFC gets only information from VOT.

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Importantly, among various functions PFC implements working memory so it is capable of remaining active for sometime after certain signals reaching it fade away. To simulated this, in the model the PFC is a map of leaky neurons activated one-by-one by the corresponding neurons of VOT. Formally, each PFC neuron activates as follows:

$$a_{j(PFC)}[t + \Delta t] = \chi a_{j(PFC)}[t - \Delta t] + (1 - \chi)a_{j(PFC)}[t] \quad (6)$$

where $a_{j(PFC)}[t]$ is the activation of neuron j of PFC at time t , Δt is the integration step (Δt was set to 0.01 sec), χ (χ was set to 0.7), is a parameter used to weight the contribute of both the past $a_{j(PFC)}[t - \Delta t]$ and current neuron activation $a_{j(PFC)}[t]$ in the computation of the next neuron activation $a_{j(PFC)}[t + \Delta t]$. Pilot tests showed how this leakiness of PFC neurons also allows avoiding that the PFC inhibitory and excitatory signals suppress the signals reaching the PMCI via the dorsal pathway too early, namely before they have an effect on RTs.

Learning mechanisms

The model is trained in sequence in two learning stages which roughly correspond to the main relevant learning phases experienced during life and during the experiment by real participants. Initially, the weights of all the plastic connections were set to values randomly chosen in the range [0, 0.1].

Phase 1. Learning to interact with objects during life

The first learning phase which simulated learning to grasp objects experienced by real participants during life. This phase led the model to acquire the affordance-based behaviour within the dorsal stream (in particular, this process updated the AIP-PMCI connections; cf. Rizzolatti, Luppino, & Matelli, 1998) and to form the identity of objects within the ventral stream (in particular, it updated the VC-VOT connections; cf. Rodman, 1994).

The training was performed by repeatedly presenting one by one the eight objects of the experiment to the model (trials). For each object presentation we systematically varied the colour of the object (either the colour of the target or the colour of the distractor), and its position in space (either the central position or one of the two peripheral positions). At each object presentation, VC performed colour-based edge detection of the object image and AIP performed colour-independent edge detection.

The AIP-PMCI connection weights were updated on the basis of a “motor babbling” process and a Hebb covariance learning rule. This allowed the dorsal pathway to acquire the capacity to perform the correct grasp depending on the shape of objects. Motor babbling processes (von Hosten, 1982; Caligiore et al., 2008) are general learning processes for which the production of rather unstructured behaviours allow the formation of basic associations

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between sensory representations and motor representations (Piaget, 1952). The motor babbling process was implemented here as follows. (a) one presented object was set close to the hand palm of the system; (b) during the trial steps, the two angles of the hand were progressively decreased of two degrees at each step: this led the PD muscle models to close the hand around the object: this process captures the essence of a random exploration (cf. Caligiore et al., 2008), plus a learning taking place only in case of success (see next point); (c) when the thumb, index, and medium finger tips were in touch with the object the association of the patterns of activation of AIP and PMCI was performed on the basis of the covariance Hebb rule indicated below: this mimics a simple trial-and-error learning where learning processes are triggered only in case of successful movement (cf. Berthier, Rosenstein, & Barto, 2005).

When learning was triggered, the all-to-all connection weights between AIP and PMCI neurons were updated on the basis of a Hebb covariance learning rule (Sejnowski, 1977; Dayan & Abbott, 2001) so as to form associations between the perceived shape of the object (AIP) and the corresponding hand posture (PMCI). Formally, the Hebb rule was as follows:

$$\Delta w_{ji} = \eta (a_j - \bar{a}_j)(a_i - \bar{a}_i) + \zeta a_i \quad (7)$$

where η is a learning rate (η was set to 2), w_{max} keeps the connection weights within a small range (w_{max} was set to 0.15), a_j is the activation of the PMCI neuron j , a_i is the activation of the AIP neuron i , \bar{a} is the moving decaying average of the activation of neurons \bar{a}_j or \bar{a}_i (ζ was set to 0.8; \bar{a}_j or \bar{a}_i were set at zero at the beginning of each trial). This rule strengthens the connections between each couple of neurons which have both an activation above or both an activation below their own average activation, and weakens their connections in other cases. Note that although simple this process allowed the system to store various grips with different apertures depending on the different size of objects.

During motor babbling trials, the ventral stream acquired the capacity to categorise objects on the basis of their appearance. In particular, the VC-VOT connection weights formed the categories of objects on the basis of a Kohonen learning rule (Kohonen, 1997; Ritter, Martinetz, & Schulten, 1992):

$$\Delta w_{ji} = \mu \exp \left[- \frac{\|v_{jmax} - v_j\|^2}{2\sigma^2} \right] w_{ji} \bar{v}_i \quad (8)$$

where μ is a learning rate (μ was set to 1), v_j is the vector point corresponding to the position of the VOT neuron j whose incoming weights are being updated in the map VOT, v_{jmax} is the vector point corresponding to the position of the VOT neuron with maximum activation in the map (“winning neuron”), σ is the width of the Gaussian activation function of

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VOT neurons (σ was set to 0.55), a_i is the activation of the VC neuron i , w_{ji} is the connection weight between the VC neuron i and the VOT neuron j .

Phase 2. Learning to accomplish the experimental tasks

The second learning phase mimicked the development of knowledge within the ventral pathway necessary for accomplishing the psychological experiment. This learning phase involved repeated interactions with the objects presented in isolation (either the target or the distractor). At each step of a trial, these processes took place: (a) the model perceived the object (the target at the central position or the distractor at one of the two peripheral positions): this activated the VC, the AIP, the VOT, and the PFC; (b) if the perceived object was the target, the PMCI was activated so to perform the grip requested by the psychological tasks (power grip for straight objects, precision grip for spherical objects); this amounts to assuming that the correct grip, dependent on the experimental instructions and apparatus, was performed thanks to memories and processes related to such instructions not explicitly simulated here as not relevant our goals; if the perceived object was a distractor, the PMCI was activated so to perform the grip according the affordance evoked by the object (power grip for a large distractor, precision grip for a small distractor), so always in agreement with the signal coming from the AIP; (c) if the object was the target, the weights of the PFC-PMCI connection weights were updated on the basis of the Hebb covariance learning rule of Equation (7) (in such equation w_{\max} was set to 0.35 for PFC-PMCI and η was set to 3), whereas if the object was the distractor, the PFC-PMCI connection weights were updated on the basis of Equation (6) using $-\eta$ instead of η in order to get an anti-Hebbian covariance learning (the existence of cortical anti-Hebbian mechanisms is supported by Lisman, 1989; Morán & Andrade, 1997; Tsodyks, 2002). Note that the combination of Hebbian and anti-Hebbian learning allows PFC to exert both an excitatory and an inhibitory top-down guidance of the action selection processes implemented by PMCI (Knight, Staines, Swickc, & Chaoc, 1999).

This section reports and discusses the results of the simulations directed to investigate which might be the role played by excitatory and inhibitory mechanisms on compatibility effects. The results of the simulations replicate and account for the main results of Ellis, Tucker, Symes, and Vainio (2007). Moreover, the section also presents two testable predictions on the possible consequences that damages in excitatory and inhibitory mechanisms underlying volitional movements in PD patients might have on the performance of the experiment modeled here (cf. Haggard, 2008; Knight et al., 1999).

During the experiment, the simulated participants were shown scenes containing the target in a central position and the distractor in one of the two peripheral positions. In the original experiments the two objects a first were presented with the same colour and assumed the target or distractor colours only after a delay of 400 ms. This delay was introduced to “force” the participants to process both objects to a certain depth (Ellis and colleagues did not find any compatibility effect related to the distractor when such delay was not present as the participants processed only the target object). We did not use the time delay as it was easy to “force” the simulated participants and as this speeded up and simplified the simulations. All data reported below refer to ten repetition of the experiment run with different simulated participants having different initial randomly-drawn connection weights.

Insert Figure 2 about here

The model is capable of reproducing the main experimental results of Ellis, Tucker, Symes, and Vainio (2007) (see Fig. 2). Similarly to what done for the target data, we analysed the simulated data with a statistical analysis of variance (ANOVA) with the factors: target (large vs. small), distractor (large vs. small) and grip (power vs. precision). All main effects and all interactions were significant. The main effect of target ($F(1,9) = 49.72$, $MSe = 1999,444$, $p < .001$) was due to the fact that large targets ($M = 251.25$) were responded to slower than small targets ($M = 180.75$); the effect of distractor ($F(1,9) = 21.95$, $MSe = 875.55$, $p < .001$), was due to the fact that processing large distractors ($M = 200.5$) required less time than processing small distractors ($M = 231.5$). Both results differ from those found in the target experiments, but this was not a target of this study. The main effect of grip reflected the results found

PREPRINT: 22.Caligiore D., Borghi A.M., Parisi D., Ellis R., Cangelosi A., Baldassarre G. (2012). How affordances associated with a distractor object affect compatibility effects: A study with the computational model TRoPICALS. *Psychological Research*, 77(1), 7-19. doi 10.1007/s00426-012-0424-1 with human participants ($F(1,9) = 5.64$, $MSe = 2680,55$, $p < .05$) as precision grip responses ($M = 202.25$) were faster than power grip ones ($M = 229.75$).

The interaction between target and distractor was significant ($F(1,9) = 19.07$, $MSe = 1475$, $p < .005$). Post-hoc Newman-Keuls tests showed that, while with small targets there was no difference between distractors, with large targets an congruency effect was present as RTs were faster with large distractors ($M = 217$) than with small ones ($M = 285.5$) (Newman-Keuls, $p < .0001$).

The interaction between target and grip was significant ($F(1,9) = 148.20$, $MSe = 1603.33$, $p < .001$). Post-hoc Newman-Keuls tests showed that all comparisons were significant. These results confirm those by Ellis, Tucker, Symes, and Vainio (2007): responses are faster when the target is compatible with the grip affordance, and slower when the response is incompatible with it. The advantage of compatible pairs was particularly marked with small targets which elicited a precision grip.

Post-hoc Newman-Keuls on the interaction between distractor and grip ($F(1,9) = 40.82$, $MSe = 1249.44$, $p < .0001$) showed that, while with large distractors responses with power grip ($M = 239.5$) were significantly slower than those with precision grip ($M = 161.5$), with small distractors the advantage of the precision grip ($M = 220$) versus power grip ($M = 243$) did not reach the statistical significance. Even if with some differences, the overall pattern of results is similar to the one found by Ellis, Tucker, Symes, and Vainio (2007) and confirm the presence of a negative compatibility effect.

Neural mechanisms underlying target and distractor effects

The target-related compatibility effects showed on Fig. 2 can be accounted for by considering that in the target-incompatible trials the processing of the target by the ventral pathway (VC-VOT-PFC-PMCl) evokes an action different from the action evoked by the dorsal pathway (VC-AIP-PMCl) (e.g., a precision grip to categorise a large cylinder), thus causing a conflict within the PMCl (Fig. 3a). As the PFC-PMCl signal is stronger than the AIP-PMCl signal, the excitatory bias from PFC wins the competition (e.g., by triggering a precision grip to correctly categorise the large cylinder) but the resulting RTs are relatively long. Indeed, when PFC and AIP signal clusters mismatch they lead to a slower charge of the PMCl leaky neurons which will win the competition, so these neurons will take longer to reach the threshold required to trigger the action. Instead, in the target-compatible trials (Fig. 3b) the signals from PFC and AIP will match and converge onto the same action represented by the neurons within PMCl, these neurons will rapidly charge and reach the action triggering threshold, and so the RTs will be relatively fast.

Insert Figure 3 about here

The distractor effects showed on Fig. 3 can be explained considering that the processing of the distractor by the ventral pathway (VC-VOT-PFC-PMCl) always send signals to the neurons representing the same action recalled by the dorsal pathway (VC-AIP-PMCl) by the same object, but such signals travel along inhibitory connections (indeed, these connections are developed during by the participants to precisely to inhibit the affordances when these should not lead to an action execution). When the action requested by the experiment is the same action evoked by the distractor, the inhibition from the distractor tends to inhibit such action and this results in longer reaction times.

As an example, consider the case reported in Fig. 3c related to a distractor-compatible trial where the action requested by the experiment is the same action evoked by the distractor: a power grip to categorise a straight target object (a small cube) with a large distractor (cylinder). In this case, the inhibition caused by the distractor via the ventral pathway fully inhibits (as it is larger) the affordance-related activation caused by the same distractor along the dorsal pathway. However, such inhibition in part also inhibit the target-related activation travelling along the same ventral pathway and so slows down the production of the action requested by the psychological experiment (also note the excitation caused by the precision-grip affordance of the target caused via the dorsal pathway, incompatible with the power-grip action requested by the same target to accomplish the task).

Predictions of the model: compatibility effects in Parkinson's disease (PD) patients with damages in the volitional movements circuits and the action selection circuits

We used the model to simulate the dopamine deficit impairments caused by PD on the circuits involving the loops formed by BG with the pre-SMA, the cortical “bridge” which allows the PFC to exert voluntary executive control on the PMCl, and also the dopamine deficits that PD produces on the BG loops that allow PMC (and motor cortex) to perform action selections. Assuming that the first type of damage renders both the PFC-PMCl excitatory and inhibitory biases less effective (Jahanshahi et al., 1995), we reproduced the impairments in the model by reducing the maximum absolute value achievable by the connection weights of the PFC-PMC pathway (w_{\max} was changed from 0.35 to 0.25). Assuming that the second damage renders the action selection process of the BG-PMCl loops less effective, in particular that the lower dopaminergic levels imply a less effective disinhibitory mechanism within the BG (Lang & Lozano, 1998; Redgrave et al., 2010), we simulated this damage by reducing the strength of the excitatory signals which fuel the dynamical competition within PMCl (α of Equation (4) was set from 1.2 to 0.5). The training processes

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used for the intact model were also used with the lesioned models.

Fig. 4a and 4d show target- and distractor-related compatibility effects exhibited by PD patients simulated by TroPICALS by implementing both impairments described above, or either one of the two impairments. The data related to the both-lesioning condition can be considered to represent the condition of real PD patients. The data related to the single lesion could not be possible obtained with real patients and are obtained thanks to the possibility of implementing focussed lesions in the model. This tests are important as they allow to isolate which specific aspect of complex diseases, such as the PD, affect the observed behaviour. The data reported in the figures and analysed below refer to average data obtained by repeating the experiment with ten different simulated participants for each lesioning condition.

Insert Figure 4 about here

As in the baseline simulation, we performed an ANOVA analysis with the factors: target (large vs. small), distractor (large vs. small), and grip (power vs. precision). When both circuits were lesioned, only the single factor-effect related to the grip was significant ($F(1,9) = 7.75$, $MSe = 318985.56$, $p < .03$): RTs were slower with power ($M = 923.00$) than with precision grip ($M = 571.25$). The interaction between target and grip was significant ($F(1,9) = 48.90$, $MSe = 356991.12$, $p < .001$), indicating that the compatibility effect was preserved. Interestingly, the distractor effect was no more significant.

Passing to analyse the data related to the single lesioning condition, in the ANOVA in which only the BG-preSMA circuit was damaged the effect of the distractor was preserved: large distractors ($M = 235.50$) were processed faster than Small ones ($M = 292.75$; $F(1,9) = 7.28$, $MSe = 9004.03$, $p < .05$). In addition, the interaction between target and grip was significant ($F(1,9) = 134.46$, $MSe = 7117.36$, $p < .001$), indicating that the compatibility effect was preserved. Finally, the 3-way interaction between target, grip, and distractor was significant ($F(1,9) = 6.15$, $MSe = 9042.92$, $p < .05$); post-hoc Newman-Keuls tests revealed that with large targets, irrespective of the distractor size, power grips are faster than precision grips ($p < .05$); instead, with small targets power grips with a small distractor produced the slowest RTs, while the faster RTs were elicited by the precision grip, irrespective of the distractor size.

In the ANOVA applied to the data obtained by lesioning only the BG-PMC1 competitive mechanism, there were not single factor effects. However, all two-ways interactions were significant. The interaction between target and grip ($F(1,9) = 12.59$, $MSe = 267184.59$, $p < .01$) indicated that the target compatibility effect was preserved, even though post-hoc Newman-Keuls did not reveal any significant difference. The significant interaction between target and

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distractor ($F(1,9) = 6.22$, $MSe = 21461.25$, $p < .05$) was due to the fact that the incompatible combination “large target-small distractor” produced the slowest RTs (Newman-Keuls, $p > .05$). Finally, the interaction between distractor and grip ($F(1,9) = 7.47$, $MSe = 23520.14$, $p < .05$) revealed that, with the precision grip, large distractors were faster than small ones (Newman-Keuls, $p < .05$).

These analysis highlight some important points. First, the model with both lesions (most similar to a fully expressed PD damage) predicts that the PD patients having a level of impairment comparable with that of the model would still exhibit target-related compatibility effects while failing to exhibit distractor-related negative compatibility effects. Second, the simulations related to the specific damages caused by the PD revealed that the damage of the PFC-(preSMA)-PMC pathway is not sufficient to eliminate the distractor-related (negative) compatibility effect as the lower “volitional signals” related to the target and the distractor and supported by this pathway are still enough to exert an influence on action. Last, the damage of the BG-PMC circuit, which underlies the integration of information from various sources and implements action selection as an outcome, would leave the target-related effects intact whereas would impair the distractor-related ones. The reason would be that the higher total inhibition of system due to lower dopamine levels would lead to mask the differential effects produced by the inhibitory signals related to the compatible or incompatible distractors.

Conclusions

This paper presented an enhanced version of the embodied computational model TRoPICALS. Caligiore et al. (2010) showed that TRoPICALS, thanks to the constraints used to formulate its overall functioning principles and specific assumptions (neuroscientific data, behavioural data, embodiment, and reproduction of learning processes), was able to replicate the results of a number of experiments on compatibility effects, to provide a neural-based account of such results, and to advance new predictions to test in novel experiments. The present work shows that TRoPICALS also replicates and accounts for further results on compatibility effects obtained with a contextual presence of a target and a distractor, and allow the formulation of specific predictions on the possible outcome of the same experiments if run with Parkinson Disease patients.

The major novelty of the present work is that TRoPICALS led to formulate the hypothesis for which two different circuits connecting the prefrontal cortex to motor areas, one excitatory and one inhibitory, are involved in the accomplishment of task responses when both target-objects and distractor-objects are presented. This hypothesis enhanced the model in two ways. First, it allowed to replicate and provide a brain-based neural account of the results obtained by Ellis, Tucker, Symes, and Vainio (2007) on compatibility effects in presence of distractors. Such account is based on the idea that the prefrontal cortex might play a double role in its top-down guidance of action selection: (a) a positive bias in favour of the action requested by the experimental task; (b) a negative bias directed to inhibiting the

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action automatically evoked by the distractor (Knight, Staines, Swickc, & Chaoc, 1999). This proposes possible different neural circuits underlying facilitatory and inhibitory effects studied in literature on compatibility effects.

The hypothesis on the excitatory/inhibitory connections linking the prefrontal cortex to motor areas also had a second advantage: it allowed us to advance specific predictions on the behaviour that PD patients with damages in both the excitatory and inhibitory mechanisms would exhibit in the target experiment. The prediction indicates that: (a) target-related compatibility effects are still present in PD patients (in line with Oguro, Ward, Bracewel, Hindle, & Rafal, 2009); (b) distractor-related compatibility effects would tend to disappear in the PD patients mainly due to the overall higher inhibitory effects caused by dopamine depletion caused by the disease.

Overall, we believe that the results presented here have a number of relevant implications for the literature on compatibility effects and on its implication on the issues of how knowledge on objects and the world is represented in the mind. First, the replication of the experimental results on compatibility effects in the presence of distractors provide a neural-based account of the mechanisms underlying them. Second, the model allows producing specific predictions that can be verified with PD patients. In this respect, the possibility of separately lesioning different circuits as it happens in PD allows understanding which specific aspects of it produce which specific effects on behaviour and knowledge representation. Third, the finding for which with PD-like lesions the main target-related compatibility effects are preserved while the distractor-related ones tend to disappear has important theoretical implications as it suggests that the excitatory mechanisms underlying compatibility effects are more prominent and robust than inhibitory ones. Importantly, note how all these results point to the fundamental role played in cognition by the embodied/action-based components of the internal representations of objects. These components are both related to the affordances of objects and to the specific actions that can be implemented on them, or *should not* be implemented on them, on the basis of a prefrontally-driven higher-level cognitive processing.

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Figures and captions

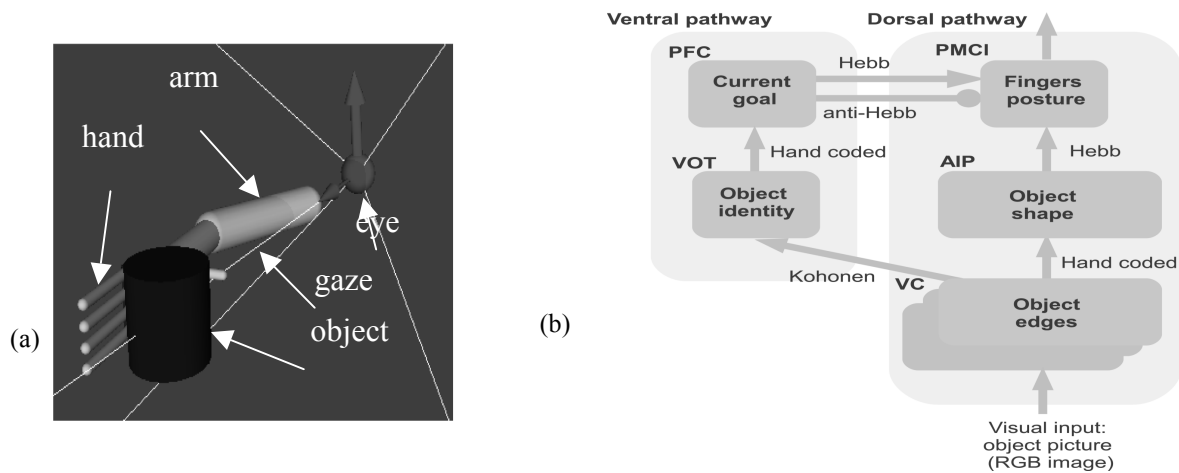


Figure 1: (a) The simulated arm, hand, and eye interacting with a simulated cylinder. The line passing through the object indicates the gaze direction whereas the other four lines indicate the range of the scope of the eye visual field. The hand works on the horizontal plane. (b) Architecture of the modified TRoPICALS model used in this work. The input of the system, the VC, is formed by three RGB neural maps encoding the edges of objects; each of these maps is divided in three visual regions (one foveal region and two peripheral regions). Downstream the VC, the model divides into two main neural pathways: the dorsal pathway, which implements suitable sensorimotor transformations needed to perform action on the basis of perception, and the ventral pathway, which allows flexible control of behaviour thanks to the biasing effects exerted by PFC on action selection. The figure highlights the hardwired connections and the connections which are updated with learning processes based on a Hebbian or an anti-Hebbian covariance learning rules, or on the basis of a Kohonen learning rule.

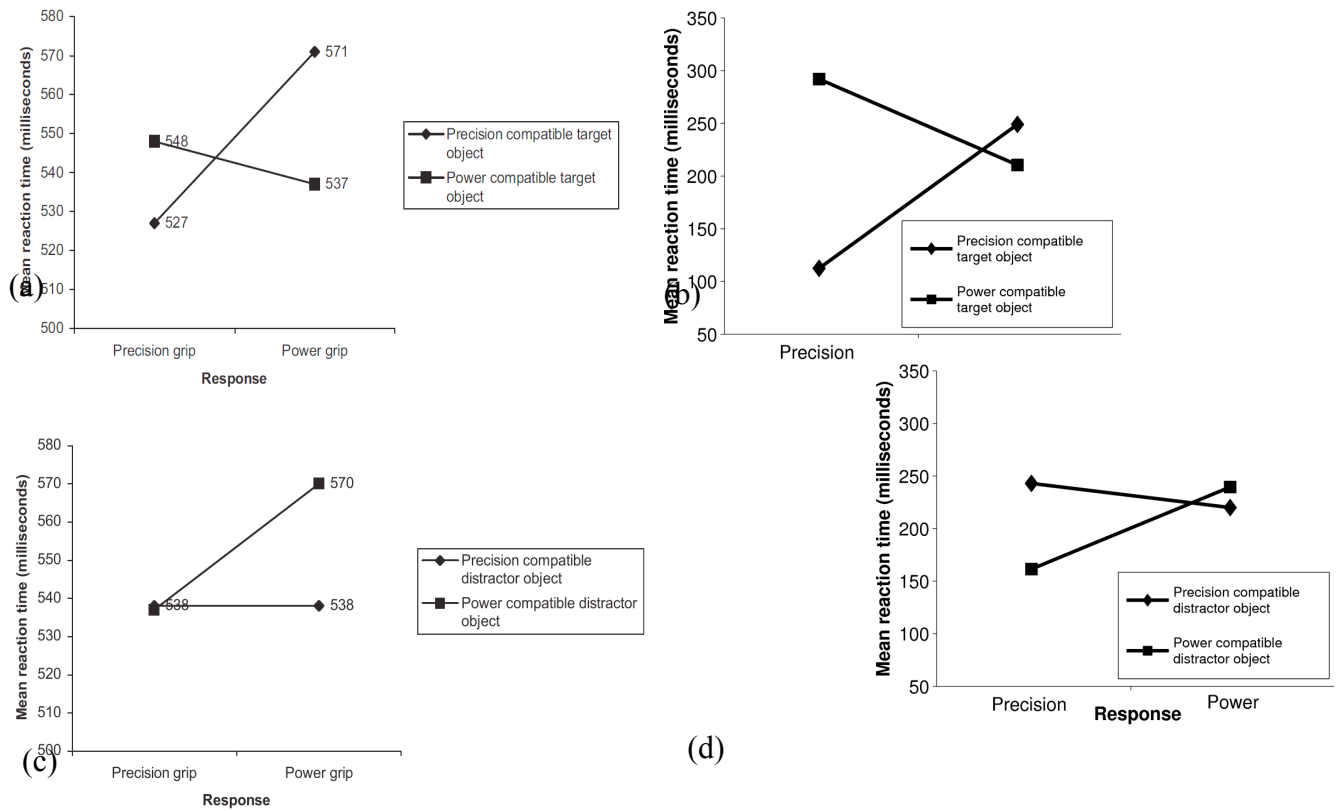


Figure 2: Average reaction times (y-axis) versus kind of grip (x-axis). (a, c) Data from real participants of the experiments of Ellis, Tucker, Symes, and Vainio (2007) (reproduced with permission, copyright of xxxx). (b, d) Data produced by the simulated participants. (a, b) Data relative to the target-based compatibility effects. (c, d) Data related to the distractor-based compatibility effects.

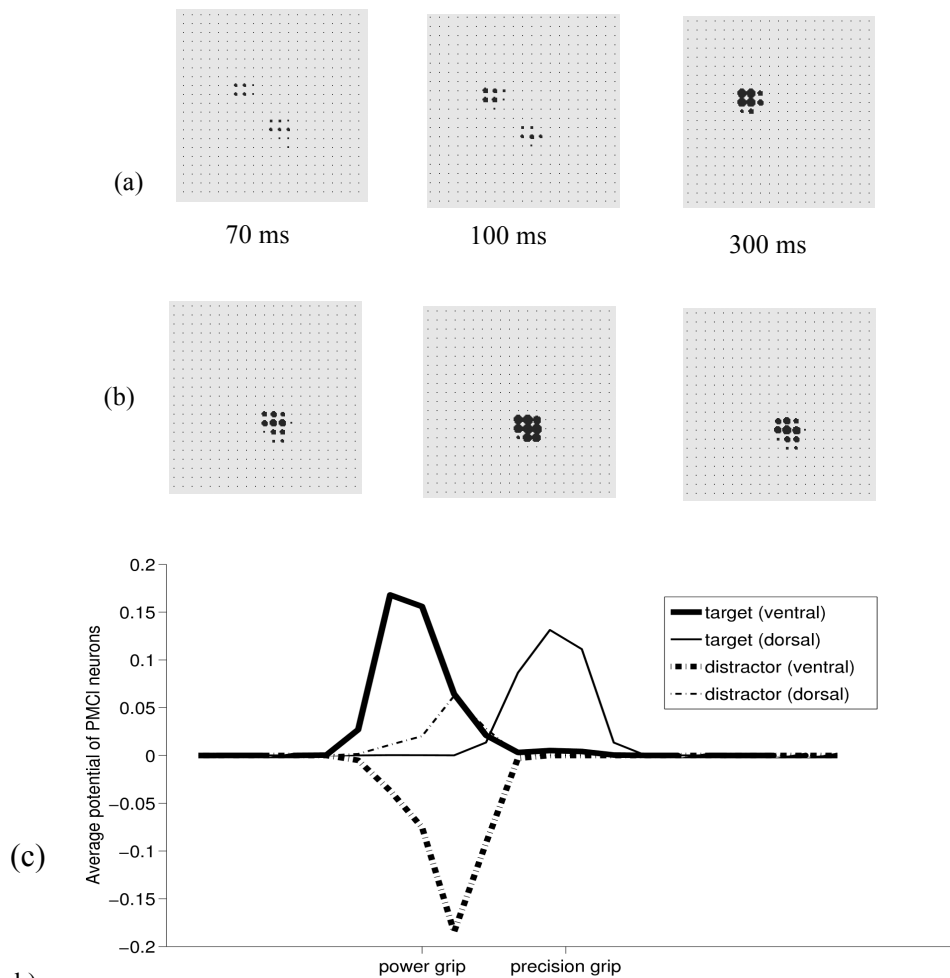


Figure 3: (a-b)

Neural mechanism underlying target-related compatibility effects. (a) activation of the PMCI in an incongruent trial: the biases from PFC and AIP cause two different clusters of neurons to compete until the cluster caused by the PFC suppresses the cluster caused by the AIP and triggers the suitable action. (b) Activation of the PMCI in a congruent trial: the biases from the PFC and the AIP overlap and cause only one cluster of neurons to compete for the expression in action. The graphs report the activation of PMCI after 70, 100, and 300 ms. (c) Neural mechanism underlying distractor-related compatibility effects: average signal (projected on one dimension of the map) received by PMCI neurons in correspondence of a scene recalling a power grip to categorise as “straight” a small cube-target, and to inhibit the automatic response elicited by a large cylinder-distractor.

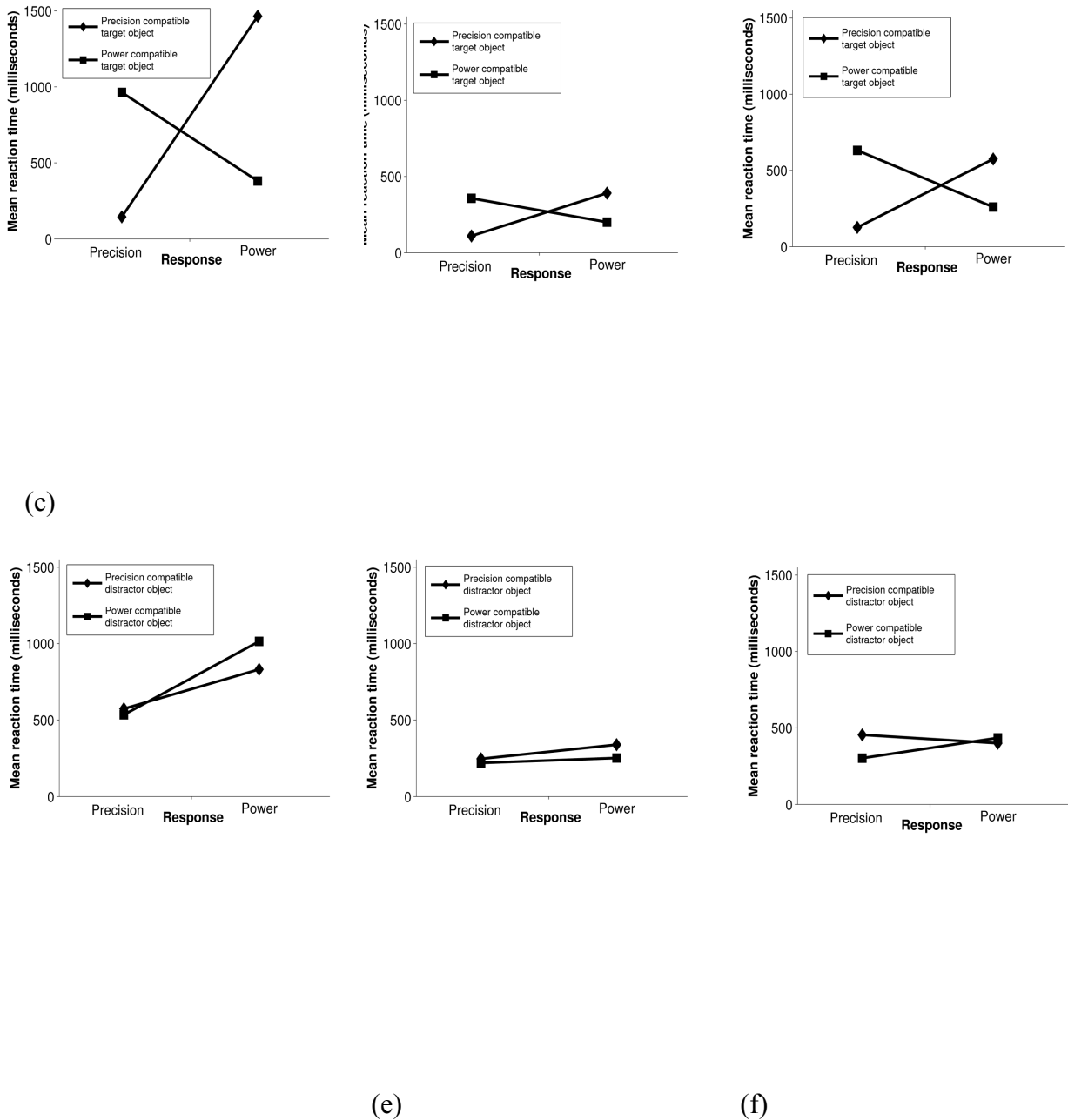


Figure 4: Average reaction times (y-axis) versus kind of grip (x-axis) for different kind of damages of PD patients simulated with the model. (a-c) Compatibility effects related to the target objects. (d-f) Negative compatibility effects related to the distractors. (a, d) Compatibility effects related to a fully lesioned model reproducing two types of PD damages: those related to the volitional PFC-preSMA-PMC neural pathway, and those related to the action-selection BG-PMC circuit. (b, e) Behaviour of the model with only the damages of the volitional PFC-preSMA-PMC neural pathway. (c, f) Behaviour of the model with only the damages of the action-selection BG-PMC circuit.