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HOW MANIPULATION-RELATED AND VISUALLY-GUIDED INFORMATION IS PROCESSED WHEN INTERACTING WITH UNUSUAL VERSIONS OF FAMILIAR OBJECTS: COGNITIVE AND ANATOMICAL BASES.

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Abstract

Object-directed actions involve properties linked to both long-term, sensorimotor representations of object manipulation (i.e. *stable* affordances) and visually-guided analysis of their structure (i.e. *variable* affordances). They are processed by the Function and the Structure systems, respectively. Aiming at clarifying how these systems are modulated during the phases of object-directed actions, *unusual* objects were created by modifying the structure of usual (i.e. traditional) familiar objects. Their function was still recognizable, but their structural variation required a greater recruitment of online visual guide, modulating the role of the two systems. A first study compared the processing of usual vs. unusual objects in a function categorization task. Results demonstrated that usual and unusual objects were both processed with the same strategy (Experiment 1), and that stable properties extended the time to "plan" the action, while variable properties were quickly processed during the movement "execution" (Experiment 2).

A second study investigated the temporal features of object processing through kinematics. Participants grasped and used the usual and unusual objects in conditions of full view or view occlusion (with or without a temporal delay). During delayed actions without vision, the effect of the rapid visual decay on kinematics was evident for usual objects, which rely more on long-term representations (Function system), while unusual objects exploited more the visual information (Structure system). Additionally, a qualitative error analysis indicated a computational interference between the two systems in the case of unusual objects.

Lastly, a functional magnetic resonance study demonstrated that categorizing unusual objects recruited more the neural correlates of both the Function and the Structure System (i.e. the ventro-dorsal and the dorso-dorsal stream, respectively) than usual objects did. Together, results demonstrated a different contribution in processing and timing of the two

systems during object-directed actions, and the theoretical relevance of using *unusual* objects.

Chapter 1

Introduction

The ability to interact with objects, even though visible in other animal species, gains a particular uniqueness when we refer to human ability of manipulating and using tools. Actually, among the animal species, the human one is the only which demonstrates to spontaneously and frequently engage itself in the use of objects. Recent cognitive and anatomical models converge in identifying two networks that are specialised in the processing of different object properties. In particular, as it will be described in the following paragraphs, models describe how the motor-related properties of objects are represented at a cognitive level, and how different cognitive systems are involved during the interaction with objects, based on distinct neural substrates.

1.1. The link between action and perception: the *affordances*

1.1.1 The ecological perspective and behind

From its first conceptualization by Gibson (1979), the concept of affordance, considered as action possibilities offered by the environment to an agent, became very popular in the field of objects and tools use, constituting an attempt to explain the human ability to interact with objects.

In this original view, the affordances were defined as a property which belongs to the surrounding environment and that is relevant only according to the properties of a certain organism acting in it: *The verb "to afford" is found in the dictionary, but the noun is not. I have made it up. I mean by it something that refers to both the environment and the animal in a way that no existing term does. It implies the complementarity of the animal and the environment"* (J. Gibson, *The ecological approach to visual perception. 1979)*

Therefore, the affordance does not define the object, but the result of a process consisting in an agent perceiving the object. The perception is unique for every organism, due to its relationship with the environment and to its action possibilities.

Gibson is the ancestor of the ecological approach, according to which, perceiving the affordances relies on the agent's ability to extrapolate the surrounding environment's invariable information. This perceptual process would be characterized by a certain level of flexibility, which makes it an adaptive mechanism to interact with the world. Indeed, the same object can provide different affordances, and the need to achieve a desired state would guide the organism toward the most appropriate affordance which allows to establish a goal and the way to reach it at a specific moment (Michaels, 2003). The crucial point of this approach, however, is that the perception leads to the action without the mediation of any cognitive representations in the between, that is all the information needed to act is conveyed by the perceived object.

The definition of affordance has been widely accepted by the scientific community, mainly because it gathers a fundamental part of the mechanisms on which the functioning of our brain relies, that is the strong link between the perceptual and the motor systems.

The experimental evidence supporting such a kind of link demonstrated that objects processing induces the potentiation of the action afforded by the object. In other words, when an object is perceived, action relevant properties of that object facilitate motor responses congruent with those properties (Tucker and Ellis, 1998, 2001; Ellis and Tucker, 2000; Phillips and Ward, 2002). In 1998, a well-known study by Tucker and Ellis demonstrated that the orientation of the object's graspable part affected motor responses. A graspable object was presented with the handle orienting to the right or to the left. Participants were asked to judge whether the presented object was upright or inverted, by pressing a right or left key. An action potentiation induced participants to faster responses when the they responded with the hand spatially corresponding to the object's handle orientation (i.e. responding with the left hand to a left-oriented object handle), compared to when they responded to the handle orienting to the opposite side. This effect was referred to as the *affordance effect*.

Importantly, besides the intention to act, even the mere and passive observation of a graspable object's picture activates brain regions associated with motor processes (Chao and Martin, 2000; Grezes and Decety, 2002).

Ellis and Tucker (2000) proposed that the affordances consist in dispositional properties of the observer's nervous system, rather than in dispositional properties of objects and environmental events. In particular, the nervous system makes the affordance-related information available by involving the motor system in the object visually-derived representations. Therefore, the relevant parts of an object would be potentiated by visual perception and would elicit corresponding motor patterns required to grasp it. The authors define such a kind of low-level associations between the object and the actions evoked by its components with the term *micro-affordances,* referring to simple motor representations which follow the attentional focus on the object (see also Vainio, Ellis and Tucker, 2007) and which are limited to visuomotor primitives common to several different actions. Moreover, these primitive motor representations, automatically activated regardless the agent behavioural goals, would refer to specific action components.

Therefore, according to Gibson's ecological approach, the aim of perception is to guide action: every organism differently perceives the environment, according to the chances of action it offers to that particular organism, or, in other words, according to the possible actions the organism has the chance to act. In these terms, the way in which an organism acts depends on the way it perceives the surrounding world (Osiurak, Jarry and Le Gall, 2010). Tucker and Ellis proposal, instead, claims the interdependence between perception and action. In particular, in the visually-derived object representations, an involvement of the motor system is observed: Vision is able to affect our actions, but the motor system sends information to the visual system as well. In this way, our representations about the world would fit our abilities to act on it (Tucker and Ellis, 2001).

At last, while the gibsonian view (Gibson, 1979) is fundamentally anti-representational, Tucker and Ellis (2000) insert the concept of affordance in an *embodied* perspective, by defining the affordances as the coupling of motor and visual experiences which occurs in our brain.

1.1.2. A new classification: *Stable, canonical* and *variable* affordances.

If affordances are considered, as said above, in an *embodied* perspective as the combined product of the visual and motor activations, one consequence is that the relationship between the organism and the environment is represented by the way the acting organism processes the surrounding world at a cognitive level. On the one hand, this view sticks to Gibson's view, highlighting the relevance of interactions between the environment and the organism considered as a whole. On the other hand, it focuses not only on the dynamics of this interaction, but also on the way they are neurally represented. This is the most diverging point in relation to the externalist and anti-representational gibsonian perspective (Borghi and Riggio, 2015).

Indeed, previous studies on the automatic activation of affordances focused on the stimulus visual processing and did not specify whether different kinds of affordance exist and how they are neurally represented (Borghi and Riggio, 2009; 2015).

For example, the study by Tucker and Ellis (1998) demonstrated how the visually-derived affordances (i.e. object handle orientation) affected the overlapping lateralised responses, i.e. the left or right oriented handle facilitates the responses performed with the spatially congruent (left or right) hand. In this case, the handle orientation is not a permanent object feature, but it has to be processed on-line. Therefore, a temporary feature, processed online, was used to adapt the motor response (Borghi and Riggio, 2015).

Differently, in one of their studies, Borghi and colleagues (Borghi, Bonfiglioli, Lugli, Ricciardelli, Rubichi and Nicoletti, 2007) demonstrated the existence of a compatibility effect due to the correspondence between the kind of grasp showed by a prime stimulus and the grasp actually required by the target stimulus. They asked the participants to perform a natural/manmade object categorization task, where the object-related grasp was a task-irrelevant feature. In particular, this effect was observed only when participants had been previously trained to manually perform the grasp associated with the prime stimulus. In this case, the observed effect was based on an invariable object property (i.e. size), which evoked a quite stable grasping action. The association between this visual property and the motor response it evoked could be built in a long-term memory stored representation. This does not mean that the online processing is excluded. Rather, the stable parameters used for action programming (especially for the off-line programming) are taken into account and they cannot be considered as mere knowledge about the object, because, as in the case of the variable features, they are able to dynamically evoke motor responses.

Moreover, investigations of the object processing in the context of the language domain allowed to investigate the role of the object-directed motor simulation (e.g. Borghi and Riggio, 2009; Borghi and Scorolli, 2009; Scorolli, Borghi and Glenberg, 2009). The comprehension of sentences containing action verbs has been demonstrated to evoke a motor prototype which includes not only the grip we usually adopt to grasp the object but also the typical orientation we are used to face with when we use it. Indeed, it has been shown that the time required to recognize an object is influenced by the incongruence between the canonical (stored in a long-term representation) and the variable (online processed) information, leading to faster response times for typically-oriented objects.

In general, these results led to the conclusion that the object's relevant features evoke different affordances that can be dissociated. According to Borghi and Riggio (2015), affordances can be distinguished on the base of the reliance on the context of an object property. This vision integrates visual and motor experiences and considers how agent-object interactions are represented at a neural level. On the base of the components of an action, affordances can be divided in *stable*, *canonical* and *variable*. Stable affordances derive from the invariable features of the object and from its relationship with the agent (e.g. object size). The association between the object visual properties and the motor response they elicit can be stored in memory: For example, the size of a cherry and the precision grip required to grasp it (Borghi and Riggio, 2015). They emerge from a slow, off-line visual processing of the object, based on the stored knowledge built up by the experience. *Canonical* affordances refer to object's properties which are stable to a lesser extent than the stable ones. Indeed, they are characterized by a certain level of variability, but they are related to the actions we most commonly perform on an object, to the context in which we most commonly find an object and to the most common goal we achieve with an object. For example, while object orientation can vary across the contexts, the typical orientation it presents when we interact on it (e.g. the upright orientation of a mug) is considered a canonical affordance. In particular, the object "canonicalness" is not linked to perceptual factors, but to functional (use-related) object features, which rely on a representation built up on previous experiences. Therefore, *canonical* affordances can be considered as a subset of stable affordances. At this regard, it has been demonstrated that language processing involves the activation of a motor prototype which represents stable and canonical affordances, but not the variable ones (Borghi and Riggio, 2009).

Lastly, *variable* affordances are properties which need to be elaborated *ex novo* every time we face with the object, because they rely on the context at the maximum level and are related to the action to be performed. Again, it is the case of object orientation, a property that is always different across situations and that needs to be constantly updated, such as the orientation of the handle of an object. They emerge from a fast, online visual processing (i.e. during the actual interaction with the object), which continuously updates the visual information and defines the current state of the object.

To note, the authors highlight that affordances are by no means static, but they depend on the variations in the context, the acting organism and also on the task to be performed. The "canonicalness" of the object, moreover, demonstrates that stable and variable affordances are not defined in an absolute way, but they can be considered as varying along a continuum.

1.2. A cognitive reference for the concept of *stable* and *variable* affordances

1.2.1. The Two Action Systems model

The idea that object properties are differently represented at a neural level and supported by distinct cognitive mechanisms of object processing (as stated by the stable/variable classification), is in line with the view that interacting with objects modulates the role of specific action-related systems, according to the goal of the action that is going to be performed.

Hand-object interactions have been distinguished in two broad class of actions. On the one hand, *acting on* objects activates a schema of action based on online sensorimotor transformations and guides reaching and grasping. When we want to move an object from one place to another, such a schema of action is activated and transforms the information concerning the object features in the most suitable posture for the grip related to the transportation. On the other hand, *acting with* objects concerns the use of objects and implies the activation of schemas about skilled actions. When we want to use an object, a schema selects the over-learned grasping and manipulating gestures needed to purposefully use the object. This does not exclude the role of sensorimotor transformations, which are necessary to control the action. Rather, it means that action selection occurs on the base of known, use-related gestures (Johnson and Grafton, 2003). In these terms, the knowledge derived by previous experiences in manipulating objects is able to affect object-directed interactions and is retrieved at the sight of the object. Evidence from brain damaged patients confirmed that object-directed actions are differently affected, according to the fact that they require a knowledge about how to functionally use the object or not, i.e. whether they are based on stored representations (Buxbaum, Sirigu, Schwartz and Klatzky, 2003; see also Buxbaum 2017). During daily object-directed interactions these representations and the visually-derived information about object properties are processed in parallel and strictly integrated (Buxbaum and Kalénine, 2010; see also Buxbaum, 2017). The reason of the need of such an integration becomes evident if we consider that in most of the cases the object structure triggers different ways of grasping it. That is, an object can elicit concurrent action representations, related to the different object features. These features refer to properties of the object that are differently processed according to the action to be performed.

In 2008, Bub and colleagues (Bub, Masson and Cree, 2008) demonstrated that gestures associated with object structural metric properties (i.e. "volumetric" gestures) and gestures associated to the conventional use of the object (i.e. "functional" gestures) are able to activate distinct representations. Similarly, in 2010 Jax and Buxbaum demonstrated that grasp-to-move and grasp-to-use gestures rely on different cognitive mechanisms leading to different times in action initiation. In particular, they used the so-called "conflict objects", which require a different grasp according to the intention of using them or merely moving them, and asked the participants to reproduce the hand posture associated with a grasp-to-move or grasp-to-use action. They found that, in comparison to the non-conflict objects (i.e. objects requiring the same grasp to be used or moved), conflict-objects required more time to plan the gesture. Moreover, planning a grasp-to-use gesture required more time than a grasp-to-move gesture, leading to an increase in the time to initiate the action. These results suggest that multiple action representations were activated by the objects and that the grasp-to-use gestures required more time likely because of the activation of long-term, sensorimotor representations related to the processing of the object functional meaning.

Basing on neuropsychological evidence and on studies comparing grasp-to-use and grasp-to-move gestures, Buxbaum and Kalénine (2010) proposed the Two Action Systems model (2AS) and its revised version Two Action Systems Plus model (2AS+; Buxabum, 2017). Their model originates from the dual route models for actions, stating the existence of a direct (i.e. non-semantic) and an indirect (i.e. semantic) routes to action (e.g. Cubelli, Bartolo, Nichelli and Della Sala, 2000; Rothi, Ochipa and Heilmann, 1997; Rumiati and Tessari, 2002). In short, the 2AS model assumes that, apart from the declarative semantic knowledge (about the function of familiar objects), the interaction with objects requires a sensorimotor knowledge stored in a non-declarative form and referring to object use-related manipulation (i.e. manipulation knowledge). In parallel, also the object structural properties are processed. While the first component is elaborated by the *Function System*, the processing of the second component is carried out by the *Structure System*.

The former elicits conceptual representations of the core invariable features of the action (i.e. not varying across different instances) and associates the objects to their corresponding use-related actions. The latter, instead, serves complex visuomotor transformations, continuously updating the visual information that guides prehensile actions on the objects. The two systems operate in parallel by integrating current and stored information aimed at fulfilling the planned action (Jax and Buxbaum, 2010; Bub et al., 2008). Thus, importantly, a relevant characteristic of this model is to provide a complementarity between learning-based and online processes (Buxbaum, 2017), reflecting what is implied in the distinction between stable and variable affordances (Borghi and Riggio, 2015).

These systems are also characterized by a different time course of elaboration, according to the source of information they rely on. The Function system processes the functional, long-term representations in a relative slow way, but it maintains this information active for several minutes, as a deep conceptual elaboration occurs. The Structure system, in line with its specialization in the online motor control, is based on a sensorimotor memory which rapidly decays (Buxbaum and Kalénine, 2010; Jax and Buxbaum, 2010). Thus, as described above, the execution of grasp-to-use gestures and grasp-to-move gestures implies a different recruitment of the Function and Structure Systems, respectively (see Table 1). Moreover, according to the information they process, they are also supposed to be differently recruited during interaction with familiar and novel objects (Buxbaum, 2017).

Table 1. Overview of the characteristics of the Two Action Systems. Adapted from Buxbaum and Kalénine, 2010.

Action System	Primary aspects of object coding	Activation of motor information without motor intention	Persistence of information	Relationship to conceptual knowledge	Probable mapping onto apraxia routes	Neuroanatomic substrate
Structure	Nonarbitrary "affordances" related to current visual information	Yes (motor responses may be activated outside of conscious awareness)	Short (msec)	Weak	Direct route	Dorso-dorsal stream
Function	Canonical actions; may be distantly related to structure	No (requires relevant intention/goal)	Long (min)	Strong	Indirect route	Ventro-dorsal stream

This model matches what described by the neuropsychological and anatomical evidence that supports the existence of two main anatomically and functionally distinct pathways inside the dorsal visual stream clearly involved during object-directed actions, i.e. the ventro-dorsal and the dorso-dorsal stream (Rizzolatti and Matelli, 2003; Binkofski and Buxbaum, 2013; Salazar-Lopez, 2016; Binkofski and Buccino, 2018). Indeed, ventro-dorsal stream, running from the visual areas through the inferior parietal lobule (IPL), stores visuo-kinaesthetic representations of hand-tool relationships (Kalénine and Buxbaum, 2016; Tarhan, Watson and Buxbaum, 2015), which are part of the manipulation knowledge and represent the "goal state" for the motor plans to achieve (Buxbaum, 2017). Thus, the ventro-dorsal stream has been supposed to subserve the Function System. The dorso-dorsal stream, running from the visual areas through the superior parietal lobule (SPL), instead, can adjust the content of these learned representations according to the current constraints and to the object state, since it processes visually-guided information about objects structural features and, therefore, has been supposed to subserve the Structure System (Jax and Buxbaum, 2010; Binkofski and Kalénine, 2013). The anatomical and functional distinction of these systems, together with their role in the processing of affordances, will be discussed in more detail in the next paragraph (paragraph 3). Crucially, stable and variable affordances (Borghi and Riggio, 2015) have been demonstrated to rely respectively on the ventro-dorsal and dorso-dorsal streams (Sakreida, Effnert, Thill, Menz, Girak, Eickoff et al., 2016), confirming that the affordances evoked by the objects elicit different processing mechanisms, distinct at both a cognitive and an anatomical level. However, in the model by Borghi and Riggio, stable affordances do not necessarily convey functional information during object-related actions. Anyway, given that stable affordances refer to the way we manipulate objects, it is supposed that a further specification of the stable affordances category in this term is plausible (Binkofski and Buccino, 2018).

1.2.2. The timing of affordances

As briefly reported above, the neural mechanisms underlying the processing of the stable and the variable affordances seem to operate with a different time course, in line with the nature of information they code: Long-term sensorimotor representations are slowly processed and maintained active for a relative long period of time, while structural visual information is processed on-line, but rapidly decays (Binkofski and Buxbaum, 2013). This distinction makes the difference in the time course of processing fitting for the two classes of affordances as well (Binkofski and Buccino, 2018). To date, differences in the time course concerning affordances have been demonstrated in the context of the division in "acting *on*" vs "acting *with*" objects, that is in relation with the two modalities of object interaction entailed by the 2AS model (Buxbaum and Kalénine, 2010; Binkofski and Buxbaum, 2013). Indeed, while "acting on" refers to the purpose of moving the object (i.e. of grasping it according to its structural features), "acting with" refers to the purpose of using the object and, therefore, of grasping it to perform its function.

The first evidence of this different processing time was observed in the behavioral study by Jax and Buxbaum (2010). As already shortly mentioned, they measured the movement initiation times toward two categories of objects, that were able to create or not a competition between the "move" and "use" gestures. A set of 10 conflict objects required different grasp gestures according to the goal of moving vs using them (e.g. a calculator), while the set of 10 non-conflicts objects required the same grasp for both using and moving gestures (e.g. baseball). The ratio behind their hypothesis was that move- or use-related responses would have shown the emergence of competing actions in the case of conflict objects and disentangled the contribution in time of the two streams, as they are differently recruited in moving and using objects. Participants had to release a start button and to reproduce two grasp gestures, according to the task demand. In one block, they had to reach the object placed in front of them and shape their hand as they wanted to hand it to another person; in the other block they had to reach the object and shape their hand as to use it. By counterbalancing the order of block presentation (i.e. the order of tasks), they investigated both the within-object interference and the between-task interference. Results indicated three main results, which were interpreted as reflecting the temporal characteristics of the underlying processing systems. First of all, in general, grasp responses were faster than use responses. Secondly, when the block requiring to grasp the object was presented after the block requiring its use, the grasp movements toward the conflict objects were slower in comparison to the opposite block order. Lastly, in the use task the conflict objects produced slower movement initiation times regardless of the order of task execution. Taken together, these results respectively demonstrated that: i) structure-based (i.e. grasp) responses are activated faster than the function-based (i.e. use) responses; ii) the activation of function-based responses were still active after several minutes from their activation and affected the grasp to move execution when required in the second block; iii) the activation of structure-based information rapidly decayed, as the interference with grasp-to-use gestures was not modulated by the order of tasks presentation.

Support to Jax and Buxbaum' (2010) interpretation came from Valyear and colleagues (Valyear, Chapman, Gallivan, Mark and Culham, 2011). They investigated reaction times and kinematics for responses toward 5 familiar objects (whisk, ice-scream scoop, spatula, pizza cutter, vegetable peeler) during both grasp-to-move (GTM) and grasp-to-use (GTU) actions. Their experimental design included 3 main manipulations. First, they adopted two different orders of objects presentation: a blocked presentation, in which participants had to perform only GTM actions for one entire block and GTU actions for the other block (Experiment 1), and a mixed presentation, in which before every trial an auditory signal instructed the participants about which kind of action they had to perform (Experiment 2). Second, in both the experiments they used a prime that could be congruent (i.e. the very same object presented in the following experimental trial) or incongruent (i.e. another object from the set used in the study) and that was presented 3-4 seconds before the target object. Third, the handles were identical for all the objects, so that they required the same grasp to be moved. They found that the task presentation (blocked vs mixed) was able to affect the priming effect. In turn, the prime influenced reaction times but not kinematics, indicating that the planning phase was differently modulated. In particular, in Experiment 1 (blocked presentation) they found that reactions time were faster for GTM actions in comparison to GTU actions. Moreover, while priming effect was not observed for GTM actions, for GTU actions congruent trials elicited faster responses in comparison to incongruent ones. In Experiment 2 (mixed presentation), differences in reaction times for GTU actions were still slower than for GTM actions, but, more importantly, besides the same priming effect for GTU action already observed in Experiment 1, a priming effect was observed for GTM actions too, with congruent trials eliciting faster responses than incongruent trials. Therefore, the fact that in Experiment 2 a priming effect has been observed for both the GTM and GTU actions indicates that the mixed presentation extended the access to tool identity for both the actions. The motor planning based on tool identity requires the activation of experience-based representations by the ventro-dorsal stream, which operates in a slower manner in comparison to the visually-guided object analysis carried on by the dorso-dorsal stream. In the light of the differential priming effect, three main points support the previous finding by Jax and Buxabum about the time processing underlying the processing of the Function and Structure Systems. First, reaction time for GTM actions are faster than for GTU actions, indicating that structure-based actions (i.e. involving mainly the Structure system) are faster than actions based on the processing of function-related information. Second, the concomitant absence of the priming effect only in the GTM actions of

Experiment 1 and the influence of the prime on reaction times, but not on kinematics, indicated that the motor planning phase but not the specification of motor parameters was affected. In this sense, the object processing guided by the Function system is responsible for the reaction times modulation. Third, the priming effect was observed when the responses were based on stored object knowledge (i.e. GTU actions in Experiment 1 and both GTM and GTU actions in Experiment 2) 3-4 seconds after the object prime presentation, indicating a long-lasting activation of information processed by the Function System, opposite to the short living duration of the structure-based information (as demonstrated by the absence of the priming effect in GTM actions of Experiment 1).

Besides this behavioral evidence, further literature has shown that representations elicited by language processing and by action processing mostly rely on the same neural mechanisms of action execution. Therefore, other studies tried to catch the processing timing of the Function and Structure systems, i.e. the two dorsal streams, during the processing of object-directed action representations through the language understanding and the action observation (Lee, Middleton, Mirman, Kalénine and Buxbaum, 2013; Lee, Huang, Federmeier and Buxbaum, 2018; Guerard and Brodeur, 2015). The findings helped in clarify how structure-based and function-based object processing are organized and activated during object-related actions. For example, they indicated that without minimizing the dependence from the "experience database" (i.e. the sustained vision of the target; Bub, Masson and van Mook, 2018), also the actions based on structural attributes can be driven by the stored knowledge (Lee et al., 2018). Moreover, they demonstrated that the nature of the manipulation knowledge (formed on previous experiences with objects and stored in long-term memory in the form of sensorimotor representations) processed by the ventro-dorsal stream supported the role of this stream as an interface between the ventral and the dorso-dorsal stream, sharing the way it is stored (long-term representations) with the former and the nature of its content (sensorimotor non-declarative representations) with the latter (Lee et al., 2018).

Again, they interestingly suggested that use-related action representations, activated by the Function system/ventro-dorsal stream are organized hierarchically according to the variability of kinematics that can be planned to use a certain object. It seems that the time needed to process how to use an object is affected by the specificity of the action parameters associated to it (e.g. the use of a towel is not kinematically defined as well as that use of the scissors). In particular, the use-related variability of kinematics does not depend on the level of graspability of an object, supporting the idea that acting *with* and acting *on* objects (i.e. functional and structural gestures; Johnson and Grafton, 2003; Buxbaum and Kalénine, 2010; Bub et al., 2008) involve different cognitive mechanisms (Guerard and Brodeur, 2015).

Finally, since it is still not clear whether the impairments observed in apraxic patients are due to a degraded manipulation knowledge or to a deficient ability to access this information, some studies tried to disentangle the nature of the deficits and demonstrated an abnormal speed of the manipulation knowledge activation in apraxia (Myung, Blumstein, Yee, Sedivy, Thompson-Schill and Buxbaum, 2010; Lee, Mirman and Buxbaum, 2014). This finding could account for a damage affecting the access to the sensorimotor representations of the gestures associated with the use of objects, which are then associated to the actual ability to perform those actions (Buxbaum, Kyle and Menon, 2005).

1.3. Two pathways within the dorsal visual stream

In the previous paragraph it has been said that object processing involves different mechanisms, that have been referred to two distinct anatomical pathways. Indeed, from the well-known original model stating the existence of a ventral and a dorsal visual stream (Milner and Goodale, 1995), additional anatomical and neuropsychological evidence led to propose a further subdivision inside the dorsal stream (Rizzolatti and Matelli, 2003).

1.3.1. The origins: the ventral and the dorsal streams

In 1982, Ungerleider and Mishkin proposed that visual cortical areas are organised into two distinct streams of visual information: The dorsal and the ventral streams. The former, running from the primary visual cortex (V1) to the inferotemporal cortex (IT), involving the area V4, has been defined the *what* stream as it is devoted to object perception and recognition, and to the further analysis of the object features; The latter, running from V1 to the parietal lobe, involving area V5, has been defined the *where* stream as it is devoted to the object spatial localization in the visual space (Ungerleider and Mishkin, 1982)

In this seminal model, the fundamental implication is the different contribute the two streams bring about the conscious contents of the visual experience. They play for a conscious and integrated representation of the visible world, whose contents can be employed in thoughts and actions (Briscoe and Schwenkler, 2015).

Some years later, Milner and Goodale (1995) forwarded a revised version of the two-visual-systems model, which provides for a renewed interpretation of the unity of the visual experience as it abandons the idea of a single perceptual system formed by different regions which perform specialised processes. Rather, the authors suggest considering two distinct visual worlds, which usually coincide, but that can provide different version of the reality (Turnbull, 1999). In this new perspective the two streams do not differ because of the inputs they receive, but because of the output systems they interact with. That is, both of them process object's structure and spatial localization, but they differ in the resulting percept (object vs. space; Milner and Goodale, 1995; Rizzolatti and Matelli, 2003).

The ventral stream uses the visual information to create perceptual representations able to get object invariable features and their spatial relationships, and to select a proper action sequence to interact with them. Object identification and categorization are based on these long-term, perceptual representations (vision-for-perception). The dorsal stream, instead, is specialised in the online implementation of object-directed actions (e.g. grasping and reaching actions). At this regard, it transforms the visual information that is constantly updated moment by moment into the correct coordinates for using the effector (vision-for-action). The visual control of the object-directed actions is based on these coordinates (Milner and Goodale, 1995; Milner and Goodale, 2008). With such a new functional conceptualization, the *where* stream becomes the *how* stream. In this new model, both streams are involved in the action field, but play for different roles: The ventral stream identifies the target object, so that the other cognitive systems are allowed to plan the action, whereas the dorsal stream does not select proper actions but implements them. This implementation is based on bottom-up pieces of information that: i) are available at a certain moment; ii) come from the retina (and not from perceptual high-level representations generated by the ventral stream); iii) are used to specify the action parameters, such as the trajectory and the kind of grip. In the domain of the dorsal processing, the visual information is not conscious, that is we cannot experience it, even when we are aware of the action we are performing. Moreover, the visual coding occurs according to different coordinates of references in the two streams. The ventral streams codes objects size, orientation and position relative to the other objects in a frame of reference that overlooks specific point of views, while the dorsal streams codes information in relation to the observer's point of view, that is an egocentric frame (Milner and Goodale, 2008).

Therefore, if on one hand both streams process object features and spatial information, the ventral stream focuses on the enduring characteristics of these information and uses them to identify and recognize objects, the dorsal stream, instead, visually controls the object-directed actions using the current information based on egocentric coordinates (Milner and Goodale, 2008).

1.3.2. A further division: two dorsal streams

Recently, the rigid dichotomy between ventral and dorsal systems has been criticized and anatomical and neuropsychological evidence supporting a further subdivision of the dorsal stream has been put forward (Rizzolatti and Matelli, 2003; Pisella, Binkofski, Lasek, Toni and Rossetti, 2006). Rizzolatti and Matelli (2003) proposed a further subdivision inside the dorsal stream, with two functionally and anatomically distinct dorsal streams, devoted to mediating different features of the object-directed actions: the dorso-dorsal stream and the ventro-dorsal stream (Rizzolatti and Matelli, 2003; Pisella et al., 2006; Buxbaum and Kalénine, 2010; Binkfoski and Buxbaum, 2013; Vingerhoets, 2014). The dorso-dorsal stream runs from visual area V3a and, passing through area V6 and the superior parietal lobule (SPL) and reaches the dorsal premotor cortex; it would be mostly involved in the online action control and in processing structure-based object information. The ventro-dorsal stream, instead, from high level visual areas (MT/V5) runs across the inferior parietal lobule (IPL) and reaches the ventral premotor cortex and the inferior frontal gyrus; it is considered to be involved in the processing of information relying on long term representations of object use (Binkfoski and Buxbaum, 2013; Martin, Beume, Kümmerer, Schmidt, Bormann, Dressing et al., 2016; Figure 1). Although these two streams have their own functional specializations, they show some areas of joined activation, that represent the point in which information they process is integrated. One of the candidates for carrying out this function is the intraparietal sulcus (IPS). This brain area seems to process spatial features of objects, such as orientation, which are used to prepare proper actions on them (Shikata, Hamzei, Glauche, Koch, Weiller, Binkofski and Büchel, 2003). It is supposed that the areas alongside the intraparietal sulcus make the information from IPL and SPL to converge and merge for object-oriented actions. For example, they are supposed to integrate objects´ spatial and perceptual features during grasping movements (Sakreida et al., 2016). The caudal part of the intraparietal sulcus elaborates the metric properties, such as shape, size and orientation, and the following output would be sent to the anterior part of the intraparietal sulcus to guide hand and fingers movements (Murata, Gallese, Luppino, Kaseda, Sakata, 2000; Rizzolatti and Matelli, 2003; Verhagen, Dijkerman, Medendorp and Toni, 2012). Veraghen and colleagues (2012) demonstrated that the transcranic magnetic stimulation (TMS) applied over the anterior part of IPS leads to the inability to properly organize the movement, interfering with the planning phase of a grasping movement. However, the early execution phase of the movement was not affected, rather it seemed that the ability to adapt the movement to the object orientation was impaired. Moreover, one important implication of this study is that, when the knowledge about the object is accessible, the sensorimotor system highly depends on it, which represents a first possibility of structuring the motor plan.

Neuropsychological and neuroimaging data seem to demonstrate this classification to be plausible. Indeed, on the one hand, parietal lobes architecture shows a modular organization, and on the other hand, focal brain lesions lead to impairments that selectively affect different levels of the object-directed actions, confirming that this new dorsal subdivision fits well with the wide variety of disorders following a parietal lesion (Pisella et al., 2006).

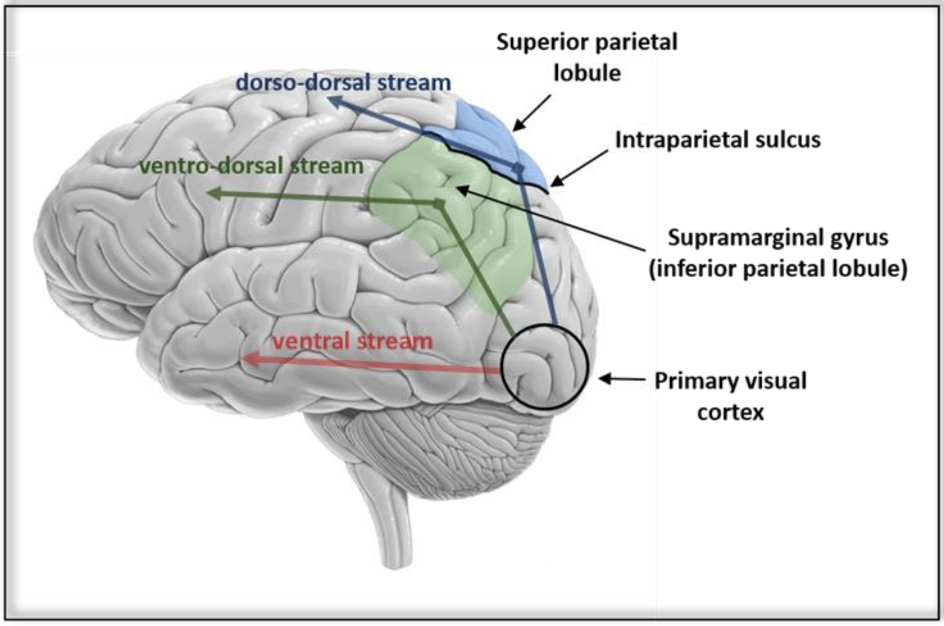


Figure 1. Schematic location of the dorso-dorsal stream (blue), the ventro-dorsal stream (green), and the ventral stream (red). Adapted from Binkfoski and Kalénine (2013).

The dorso-dorsal stream

The dorso-dorsal stream receives input from the primary sensory cortices (especially from areas coding for proprioception) and from visual areas, it is semantically blind and represents the most direct visual route to action (Rossetti and Pisella, 2002; 2003). It involves both hemispheres and constitutes a specialized network for the online, sensorimotor adaptation.

The typical disorder associated to a lesion of the dorso-dorsal stream is *optic ataxia,* characterized by the inability to point and reach objects in the peripheral vision. A crucial improvement of optic ataxic patients' performances can be observed when they are asked to reach an object with a temporal delay. This improvement is explained by a switch from an online, visually-guided processing to a memory-based, motor programming. The study of IG, a young patient who suffers from optic ataxia due to an ischemic stroke clarified the role of the dorso-dorsal stream in the visuomotor transformations and the online motor control. The online motor control supports fast modifications of motor component when grasping movements must be modified during the action execution, without causing a substantial increment in movement time and without the conscious perception of the target displacement. This mechanism has been compared to an "automatic pilot", activated by default during the execution of goal-directed actions (Pisella et al., 2000). Pisella and colleagues (2000) demonstrated that IG was impaired in automatically correcting movements in space without the intention of doing it, but her performance was normal when changes in movements were consciously programmed and based on non-spatial cues. In 2002, Gréa and colleagues (Grea, Pisella, Rossetti, Desmurget, Tilikete, Grafton, Prablanc and Vighetto, 2002) analyzed the kinematic parameters of IG's movements toward a stationary (unperturbed trials) and displaced (perturbed trials) object and compared them to those of normal controls. They found that kinematic parameters of reaching and grasping movements toward a stationary object were the same for both IG and the control group. Interestingly, the results from trials in which the target object was displaced at the time of movement onset confirmed the inability of the patient to correct online movements and demonstrated that, in terms of kinematics, she performed two distinct movements, as she had to complete the programmed movement before programming a new one according to the new target position. Indeed, according to its functional specialization, the dorso-dorsal stream continuously processes physical objects properties (e.g. shape, size, orientation) in order to calibrate proper reaching and grasping movements, without having access to objects semantics. Its function is related to movement monitoring, to grasp an object based on its current features (Brandi, Wohlschläger, Sorg and Hermsdörfer, 2014). Moreover, this system possesses a rapidly decaying, sensorimotor memory, which is not affected by the priming effect, due, for example, to exposition to congruent objects (Cant, Westwood, Valyear and Goodale, 2005; Osiurak & Badets, 2016).

The ventro-dorsal stream

The ventro-dorsal stream constitutes a system devoted to object-directed, function-based skilled actions, and involves a left-lateralized network, in line with the evidence supporting the left hemisphere's major ability to process information updates for visuomotor coordination (Martin and Dahl, 2016). Neuroanatomically, this stream seems to be an interface between the visual ventral and dorsal streams, as most of the connections coming from the ventral stream reaches the ventral part of the dorsal stream (i.e. the ventro-dorsal stream). Contrary to the dorso-dorsal online processing, this stream processes sensorimotor information coming from long-term representations of object use.

Relevant areas inside the ventro-dorsal stream are IPL and the supramarginal gyrus (SMG), which subserve the ability to use and manipulate the objects and are linked to object consciousness for action organization and recognition (Sakreida et al., 2016). In particular, the anterior part of SMG (aSMG) is considered a typically human neural substrate in the use of objects (Peeters, Simone, Nelissen, Fabbri-Destro, Vanduffel, Rizzolatti and Orban, 2009). Its activation seems to be asymmetric, with a major involvement of the left hemisphere, and several evidences showed that it is active during the execution of object-directed actions, pantomimes or imagination of use-related movements, and object-related decision-making tasks (Binkofski, Dohle, Posse, Stephan, Hefter, Seitz et al., 1998; Chao and Martin, 2000; Moll, de Oliveira-Souza, Passman, Cunha,Souza-Lima, Andreiuolo, 2000; Inoue, Kawashima, Sugiura, Ogawa, Schormann, Zilles et al., 2001; Rumiati, Weiss, Shallice, Ottoboni, Noth Zilles et al., 2004; Creem-Regehr & Lee, 2005; Johnson-Frey, Newman-Norlun and Grafton, 2005; Valyear, Cavina-Pratesi, Stiglick and Culham, 2007; Jacobs, Danielmeier and Frey, 2009; Gallivan, McLean, Valyear and Culham, 2013). Moreover, this stream is also activated by the sound produced by objects utilization (Lewis, 2005). Another important evidence comes from the selective activation of the aSMG during the observation of goal-directed actions of object use, but not during the observation of mere biological (i.e. not directed to objects) manipulations. Moreover, aSMG seems to process kinematic features of hand movements of the observed object-directed actions (Peeters, 2009). This area could therefore represent the centre devoted to the processing of the knowledge relative to the conventional use of familiar objects and to their manipulation, representing the entrance point of semantic information into the dorsal stream (Orban and Caruana, 2014).

In support of the crucial role of IPL, it has been widely demonstrated that lesions to this area are associated with apraxia for object use. Patients suffering from this disorder are impaired in using familiar objects (Heilman and Rothi, 1985), in matching objects used for the same purpose (Rumiati, Zanini, Vorano and Shallice, 2001), or in inferring the object function from its structure (Barbieri and De Renzi, 1988; see also Martin et al., 2016). Importantly, the impairment is restricted to the cognitive level, and not the motor ability (Pisella et al., 2006; Buxbaum et al., 2005). Neuropsychological studies demonstrated that IPL is devoted to process objects according to their function and to activate sensorimotor representations about how to grasp and purposefully use them (i.e. manipulation knowledge; Sirigu, Cohen, Duhamel, Pillon, Dubois and Agid, 1995; Buxbaum et al, 2003; Buxbaum, Kyle, Tang and Detre, 2006)

Buxbaum and colleagues (2003) asked apraxic patients with lesion to the left IPL to match hand postures with familiar and neutral objects. Familiar objects could be grasp with either a use posture (i.e. with the hand posture suitable to use them) or a grasp posture (i.e. according to their structure). Their performances were compared to those of healthy controls and non-apraxic, brain-damaged patients (control groups). The authors found differences between apraxic patients and both control groups in relation to familiar objects, since apraxic patients tended to select a grasp posture compatible with the structure of the objects, but not with their use. This evidence suggested that lesion to the IPL damaged the representations underlying the knowledge of appropriate hand postures for purposefully using the objects. That is, while the ability to grasp according object structure was preserved, the ability to grasp them in a "functional" way was disrupted. Some years later, these findings were confirmed in a study using the functional Magnetic Resonance Imaging (fMRI), in which the participants were asked to observe object pictures and chose, among two, the grip that they would have used to grasp them (Buxbaum et al., 2006). The authors compared the brain activations related to the Grasp condition (i.e. when participants were asked to choose the grasp fitting the object structure), the Prehensile Use condition (i.e. when participants were asked to choose the grasp suitable for the use of the object) and the Non-prehensile Use condition (i.e. when participants were asked to choose the gesture suitable for using objects, but not requiring a grip, for example a poke). Results indicated a greater activation in the left inferior frontal gyrus (IFG), posterior superior temporal gyrus (STG), and IPL when Non-prehensile Use condition was compared to the Grasp condition, whereas the comparison of Non-prehensile Use and Prehensile Use conditions revealed significant differences only in the left IPL.

1.3.3. The dorsal streams and the affordances: Evidence from neuroimaging

As described above, the candidate neural bases underlying the processing of the stable and variable affordances are the ventro-dorsal and the dorso-dorsal stream, respectively. To assess their role in processing the two categories of affordances, recently Sakreida and colleagues (2016) carried out a metanalysis of the studies on object interactions which used the functional magnetic resonance imaging (fMRI). They distinguished the studies based on stable affordances and those based on variable ones. In the category of the studies related to the stable affordances, they included the studies in which the experimental setting did not require changes in the action plan. The tasks consisted of active or observed pointing, reaching and grasping actions and involved objects that did not vary in size, shape or weight during the task performance. An example is the study by Grezes and colleagues (Grezès, Tucker, Armony, Ellis, and Passingham, 2003) in which they asked participants to perform actual precision or power grip responses in relation to the categorization of objects (requiring a precision or a power grip to be grasped) into natural or man-made. Indeed, the execution of the grasp was modulated by the size of the object (i.e. a feature eliciting a stable affordance). For the variable affordances, instead, studies including changes in the active or observed action plans, due to variations of object size, shape, weight and orientation (but not the location only) were selected. For example, Hirose and colleagues (Hirose, Hagura, Matsumura and Naito, 2010) asked participants to judge as fast as they could the graspability of 15 boxes of different size. Indeed, the response depended on the metrics of the target stimulus (i.e. a variable affordance). In total, they found 71 studies matching their criteria, 44 concerning stable affordances and 27 concerning variable ones. Their analyses focused on direct as well as on low and high-level baseline contrasts. The results showed that processing stable affordances recruited a left-lateralized network involving inferior parietal and frontal areas, whereas processing variable affordances relied on a bilateral network including dorsal areas and involving the superior parietal lobule. Moreover, the activations also revealed that the two dorsal streams present regions where their activity markedly overlapped. In particular, the intraparietal sulcus (IPS) and the superior frontal sulcus (SFS) are thought to represent converging areas in which the information coming from the two dorsal streams is exchanged and merged together for processing the final object-oriented action plans (Figure 2). Thus, this metanalysis confirmed that while stable affordances are processed mostly in the ventro-dorsal stream, the variable affordances are processed mostly in the dorso-dorsal stream.

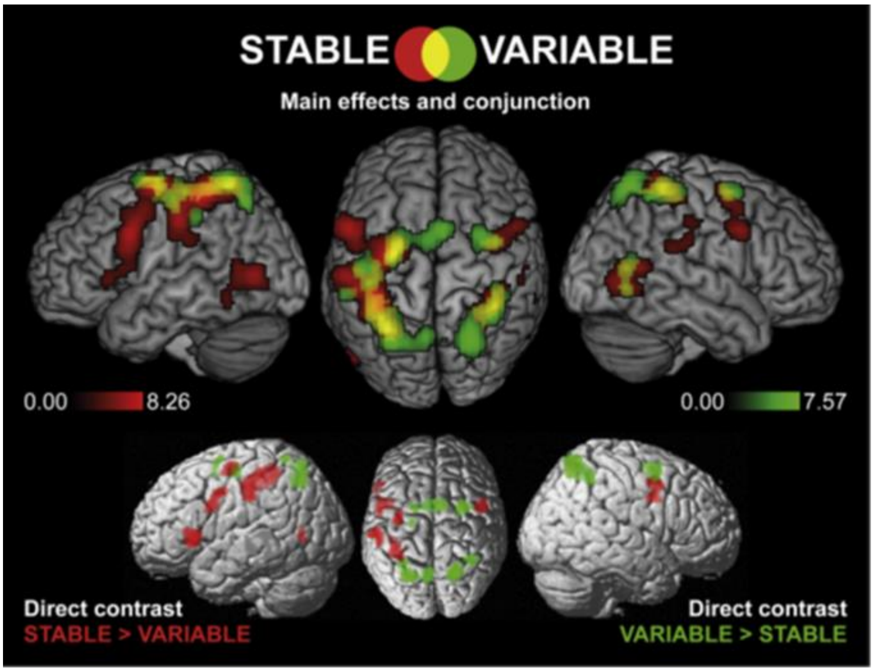


Figure 2. Above: Main effect of stable affordances (red) variable affordances (green), and conjunctive activations (yellow). **Below:** differences revealed by the direct contrasts between stable and variable affordances. From Sakreida et al. (2016).

A very recent paper from Kourtis and colleagues (Kourtis, Vandemaele and Vingerhoets, 2018) developed a fMRI experimental design in which the observation of objects induced the activation of affordances related to the long-term use-related gestures and to the immediate grasping gestures. Participants held a power grip device in one hand and a precision grip device in the other hand. They were presented by pictures of small and large objects (i.e. graspable with a precision or a power grip) at the centre of the screen, rotated so that the graspable and the functional parts pointed to opposite quadrants on the screen (i.e. a hammer with the handle pointing to the right bottom and the head pointing to the left top). When a centrally displayed arrow, pointing to the left or to right, was overlaid on the object picture, the participants were required to press the device held at the side pointed by the arrow (i.e. to press the device held in the right hand when the arrow pointed to the right, and *vice versa*). In this way, the pointing arrow was able to induce congruencies based on two different behavioural effects. The first was the “function congruency” effect and was related to the part of the object which made its function recognizable (i.e. the head of the hammer). Indeed, participants were faster in responding to an arrow pointing to the functional part of the object rather than pointing to its handle. The second was the “size congruency” effect, according to which participants were faster in pressing the device reproducing the grasp compatible with the grasp required by the observed object, although this effect was observed only in relation to small objects. Interestingly, the “function congruency” effect revealed two clusters of activation in the posterior parietal cortex (PPC), one in the SPL and a larger one in the IPL. These results are interpreted as the emergence of different type of action affordances, consistent with the concept of stable and variable affordances (Borghi and Riggio, 2015), with the functional role of ventro-dorsal and dorso-dorsal stream (Rizzolatti and Matelli, 2003; Pisella et al., 2006; Binkofski and Buxbaum, 2013), and with the processes underlying the Function and the Structure Systems (Buxbaum and Kalénine, 2010).

1.4. A particular class of stimuli: The *unusual* objects

As described in the previous paragraphs, distinct cognitive processes and mechanisms (relying on specific neural substrates) participate in the interaction with objects. Both the object structure and the stored knowledge about how to manipulate it support these processes, and actions aiming at using a single object include the retrieval of a knowledge related to its function. This thesis aims at clarifying the modulation of the cognitive and anatomical systems involved in the processing of objects, and, in particular, the role they play in the planning and execution phases of object-directed actions. Indeed, it has been demonstrated that object representations are affected by the sensorimotor experiences related to the objects (Bellebaum, Tettamanti, Marchetta, Della Rosa, Rizzo, Daum and Cappa, 2013; Weisberg, Van Turennout and Martin, 2006).

Previous studies mainly demonstrated that object properties are differently weighted according to the task demand (i.e. using an object vs moving it from a position to another) and to the familiarity of the perceived objects, that can be familiar, unfamiliar and novel (or meaningless; e.g. Vingheroets 2008; Dawson, Buxbaum and Duff, 2010; Bellebaum et al., 2013; Weisberg et al., 2007).

Instead of varying the task requirements, the ratio behind the present studies was to manipulate the ability of the stimuli to differentially recruit the anatomo-functional mechanisms related to tool use by mean of a particular class of objects. We modified some sets of familiar daily-used objects, by altering their structure. All the objects were formed by a graspable part (i.e. the handle) and a functional part (i.e. the "head" of the object, which specifies its function). Crucially, the structural variation forced the perceiver to plan new use-related movements according to the altered structure, while the object function remained undoubtedly recognizable. As a consequence, such objects can be defined neither familiar nor meaningless. Rather, they can be more considered a class of unfamiliar objects. However, in previous studies the "familiarity" of the objects was defined on the base of the knowledge about their function and previous experiences with them. That is, unfamiliar objects were defined as rare, uncommon objects. Therefore, being unfamiliar meant that their function was unknown (or perceivable; e.g. Vingheroets, 2008). Here, objects are unfamiliar because they are a modified version of usual (i.e. traditional, unaltered) objects, which are very common and whose function, as well as manipulation, is well-known. Therefore, the divergence consists of the planning phase of the movement with the purpose of using them, which has to be modified as well. We refer to these class of objects as *unusual* objects[1] (rather than unfamiliar). The choice of such stimuli has two main and interrelated implications. First, the sensorimotor representations formed by previous experiences with those objects refer to their traditional (i.e. usual) version and they are supposed not to fit with the unusual objects anymore.

[1] The idea originated from the artworks of the artistic project "The Uncomfortable" from Katerina Kamprani (https://www.theuncomfortable.com/)

As these sensorimotor representations are supposed to incorporate invariable object features, able to convey information concerning the core movements associated to their use, in the case of unusual objects an adaptation of the schema of the movement is necessary. This leads to the second implication, that is this movement "recalibration" has to be carried out on the base of the current visual information that mainly refers to object structural properties. While in the context of usual objects the sensorimotor representations refer to the (invariant) shape of the object and the visual analysis refer to temporary information (i.e. the orientation), unusual objects are supposed to induce the object structure to be treated as a "temporary" characteristic, thus requiring the contribution of the visually-driven analysis to a greater extent.

The unusual objects, together with their usual counterparts, were employed as stimuli in three studies. In all of them, the experimental task demand required to elaborate a function-related property of the objects, that was to categorize them according to their function or to grasp them in order to use them. In doing so, the function-related identity of usual and unusual objects was encouraged to be considered as the same (i.e. the unusual mug was still recognized and treated as a tool for drinking, as well as the usual mug). This request was chosen to ensure a deep processing of the objects and the access to their meaning, and, therefore, to the knowledge about the way they are manipulated (on the base of how usual objects have been manipulated during previous experiences).

Chapter 2

How to interact with unusual versions of familiar objects: The negotiation between manipulation-related and visually-guided information[2]

During object processing, the content of the perceptual information leads to an automatic activation of the motor activities driven by object features that are relevant for actions (i.e. affordances; Gibson 1979). It has been shown that such automatic motor activation is triggered even when no interaction with the object is planned (e.g. Chao and Martin, 2000; Grezes and Decety, 2002; Helbig, Graf and Kiefer, 2006; Lee et al., 2013; Gomez and Snow, 2017). Tucker and Ellis (1998) demonstrated that the reaction times (i.e. button press) provided in response to object are modulated by the orientation of their handle (i.e. the graspable part), leading to an advantage for the motor responses performed with the hand on the same side of the handle (i.e. responses with the right hand when the handle is right-oriented). On the other hand, there is also evidence that planning a grasp, based on the functional characteristics of a tool, is driven by its "head" (i.e. the part of the tool dedicated to performing the function; Skiba and Snow, 2016; Przybylski and Kroliczak, 2016; Belardinelli, Barabas, Himmelbach and Butz, 2016; Kourtis and

[2] A revised version of this chapter has been submitted to Psychological Research (Sciulli, Ottoboni and Tessari, submitted).

Vingerhoets, 2015; Pellicano, Iani, Borghi, Rubichi and Nicoletti, 2010). In addition, Pellicano and colleagues (Pellicano, Koch and Binkofski, 2017) demonstrated that object processing can also activate a high-level cognitive representation, which encodes the direction of the action (i.e. pouring liquid from a teapot to a cup), that can influence the mechanisms of response selection based on the spatial position of the portion of the object that "performs" the action (i.e. the pouring part).

As already detailed introduced in Chapter 1, Borghi and Riggio (2009; 2015) proposed an extended classification of affordance: Variable affordances referring to the information used to calibrate the movement to grasp an object and depending on the current situation during the interaction with an object (e.g. object position); Stable affordances, referring to invariant object properties, which evoke use-related gestures, stored in memory and acquired through repeated experiences with that object. This classification fits well with the Two Action Systems model (2AS; Buxbaum and Kalénine, 2010; Buxbaum, 2017), positing that interaction with objects involves two systems; A Function system dealing with conceptual representations of the core, invariable features of the action (that do not vary across instances), and associating an object to the corresponding actions; a Structure system devoted to the development of complex visuomotor transformations and guiding prehensile actions on objects. Thus, the Function system serves actions related to a purposeful use of objects (i.e. grasp to use), while the Structure system is preferentially recruited during grasp-to-move actions. The 2AS model is in line with the neuropsychological and anatomical evidence that supports the existence of (two) anatomically and functionally distinct pathways operating during object-directed actions (Rizzolatti and Matelli, 2003; Binkofski and Buxbaum, 2013; Buxbaum and Kalénine, 2010; Jax and Buxbaum, 2010; Buxbaum, 2001): A ventro-dorsal stream primary involving the inferior parietal lobule, and referring to non-declarative representations generating a mental simulation of object manipulation; and a dorso-dorsal stream, running through the superior parietal lobule, and devoted to process the objects physical features to exactly calibrate both reaching and grasping movements (Rizzolatti and Matelli, 2003; Binkofski and Buxbaum, 2013). If on one hand, the dorsal stream's specializations reflect the processing of stable and variable affordances, respectively (Sakreida et al., 2016), on the other hand, according to their characteristics, they are supposed to be recruited at a different extent, in relation to both the phase of the action and the type of object to grasp. For example, it has been demonstrated that they are recruited at distinct stages while performing an action toward a target object (Tunik, Lo and Adamovich, 2008a; Tunik, Ortigue, Adamovich and Grafton, 2008b; Rice, Tunik and Grafton, 2006; McDowell, Holmes, Sunderland and Schürmann, 2018). Moreover, actions toward familiar objects have been shown to mostly rely on experience-based, sensorimotor representations, requiring a greater activation of the ventro-dorsal stream, in comparison to unfamiliar objects (Vingerhoets, 2008; see also Buxbaum, 2017).

Previous studies also investigated the time course of object processing by comparing the intention to act on an object to use it (according to its function) or to move it from a place to another (e.g. Jax and Buxabum, 2010, 2013; Valyear et al., 2011; Osiurak, Roche, Ramone and Chainay 2013; Lee et al., 2013; Lee et al., 2018) or investigating the processing of sentences related to verbs indicating grasp-to-use or grasp-to-move actions (e.g. Wamain, Sahaï, Decroix, Coello and Kalénine, 2018). They demonstrated that a structure-based activation guiding grasp-to-move actions rises faster than the function-based activation guiding grasp-to-use actions. Moreover, the latter affects subsequent actions, indicating the capability to maintain information active for a longer period of time (e.g., minutes), while the former rapidly decays (Jax and Buxbaum, 2010). Despite the studies highlighting the temporal maintenance of activation of the two systems, none focused on their interactive role during object processing and object-directed actions. Actually, the two systems cooperate and integrate information for all the actions we daily carry on (Buxbaum and Kalénine, 2010). Distinguishing the kind of action according to its purpose (i.e. to use vs. to move) is helpful in understanding the relevant properties of object the action is based on, and, therefore, the different recruitment of the two systems. However, modulating the task in such a strict way could represent a too simplified way to infer the contribution of the two systems during daily object-directed actions in a more complex and ecological environment. In particular, what is still not clear yet is how the current (visual) information and the stored one are combined at different stages of a movement, while different classes of affordance become relevant.

In order to investigate the different contributions of the two action systems, their recruitment was modulated by manipulating the target stimuli, rather than the task. To do so, structurally modified versions of usual objects were used, in which an ad-hoc incongruence between the sensorimotor representations of object use and the online visual information was introduced. As more detailed discussed in Chapter 1, the modification kept the function of the objects still fully recognizable, but it made them uncomfortable, and unusual. Indeed, while their identity-related function is still clear, their structure does not provide stable affordances anymore, and the stored sensorimotor representations formed through experience are no longer adequate. This manipulation aimed at urging the participants to solve an ambiguity deriving from the lack of correspondence between the action-related representations - guided by the recognition of the object identity and function- and the visual information related to object structure. Indeed, the resulting (altered) structure requires modified motor plans to grasp and use them. Thus, the object's structure turns into a variable feature, which requires to be coded or adapted ex novo in the current visual context. In this way, Function and the Structure systems are differentially recruited while interacting with a still recognizable, meaningful object. The structural modification, therefore, can help in the understanding of how stimulus features are coded and the influence they have with respect to different phases of movement plan and execution.

Two behavioural experiments were carried out, in which participants had to categorize two series of objects according to their functional/semantic properties. Such a task was chosen in order to prompt participants to deeply process the stimuli and to access their functional representations (e.g. Borghi, 2004; Almeida, Fintzi, and Mahon, 2013). Experiment 1 investigated whether stable and variable affordances differ for usual and unusual objects due to the structural manipulation. Experiment 2 aimed at studying how the mismatch between the stored motor and functional representations and the new structural, online information is solved in time by investigating both the response decision and execution phases. Participants had to respond by providing an actual reach-to-grasp movement, aimed at triggering a stronger motor simulation (e.g. Bub and Masson 2010) compared to Experiment 1. Specifically, in Experiment 2 participants responded by releasing a button to reach and grasp a power grip device. By collecting both key-release and movement times, the response setting is expected to intercept the processing of the two pathways at either response-decision and execution phases (e.g. Bub and Masson, 2010).

2.1. Experiment 1

The affordance effect was investigated for both usual and unusual objects (Tucker and Ellis, 1998, 2001). The affordance effect consists of a spatial compatibility effect in which lateralized responses benefit from the orientation of the graspable part of a tool, e.g. the handle: For example, left-hand responses are faster when the tool's handle is left-oriented in comparison to when it is right-oriented and vice versa (Tucker and Ellis, 1998). This effect is based on the elaboration of variable affordances by the dorso-dorsal stream (Borghi e Riggio, 2009). Thus, we presented objects with handles orienting to either the right or the left and we asked the participants to respond in relation to a functional property of the object (i.e. whether the object is used to eat / drink or not) by pressing one of two buttons on their left or right side. In keeping with the model proposed by Borghi and Riggio (2009; 2015), we predicted that the structural variation of unusual objects would induce a computational interference due to the lack of correspondence between the stable sources of information, processed by the ventro-dorsal stream, and the structural characteristics of the object, processed online by the dorso-dorsal stream.

2.1.1. Method and Procedure

Participants

Thirty-eight, right-handed students of the University of Bologna (19 female; mean age=23,5, SD=1,64) participated in the experiment after giving their consent. All of them had normal or corrected-to-normal vision.

Ethics Statement

The experiment was approved by the bio-ethical committee of the University of Bologna in 2016, according to the Declaration of Helsinki.

Stimuli

Stimuli consisted of grey-scaled pictures of common objects (mug, fork, key, watering can) presented in two versions: a) a typical, comfortable version (usual objects); b) an uncomfortable version, but still recognizable from the functional point of view, consisting of a structural variation that modifies the grasp-to-use gesture (unusual objects; Figure 3). All the stimuli consisted of a graspable part (the handle) and a functional part (associated with their goal-related use).

Figure 3. Stimuli: Usual objects (above) and their corresponding Unusual version (below).

Apparatus and procedure

Stimuli were presented on a computer screen (17 inches, with a 1024 × 768-pixel resolution and a refresh frequency of 100 Hz) and the experiment was run using E-Prime 2.0. Participants seated in front of the computer screen and had to respond by pressing one of two lateralized keys ("x" and ".") on a keyboard, placed in front of them. After having read the instructions on the screen, they were required to position their right and left index fingers over the two lateralized keys (starting position). During each trial, a blank screen appeared for 1 sec, followed by a fixation cross lasting 1500 msec. Then, a stimulus appeared, and participants had to respond in the fastest and most accurate way by deciding whether the stimulus/object was used to feed themselves (i.e. to eat or to drink) or not. The correct answer was "yes" for the mug and the fork, and "no" for the watering can and the key. The association between the responses and the lateralized keys was counterbalanced between participants. In case of a wrong answer, an auditory signal was delivered to inform the participants about the error. Usual and unusual objects were presented in two different blocks which were counterbalanced between subjects to avoid carry-over effects during the object processing. Indeed, previous literature investigating dual-route models demonstrated that the order of stimulus presentation can mask relevant differences in their cognitive processing, because of the strategic adoption of only one of the two processing mechanisms for all the stimuli (for a discussion on the strategy selection and the effect of order of blocks in the motor domain see Tessari and Cubelli, 2014; Tessari and Rumiati, 2004; Tessari, Toraldo, Lunardelli, Zadini and Rumiati, 2015).

Each object was presented 15 times with the handle (i.e. the graspable part) orienting to the right and 15 times with the handle orienting to the left, for a total amount of 120 trials per block and 240 trials for the entire experiment. A short break every 40 trials allowed participants to rest for a while. In order to familiarize with the task, participants performed 4 practice trials at the beginning of the experiment (they were not taken into consideration in the analyses).

2.1.2. Results

Data analysis was performed using SPSS software (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp) on reaction times (RTs) of the correct responses and included within two standard deviations from each participant's mean. Only 5.95% of the total amount of trials was excluded. A repeated-measures 2x2x2 ANOVA was carried out, considering the following factors: i) Compatibility (Compatible trials vs. Incompatible trials, defined on the basis of the spatial correspondence between the right or left orientation of object's handle and the laterality of the response hand, i.e. affordance effect), and ii) Type (Usual vs. Unusual Objects) as within-subjects factors; iii) Block Sequence (the order of presentation of the types of object: Usual/Unusual vs. Unusual/Usual) as between-subjects factor.

Results showed a main effect of Type ($F(1,36)=4.427$, $p=.042$), with faster RTs for usual objects (mean= 563 ms; SD=54.8) than unusual ones (mean= 575 ms; SD= 59.12; Figure 4A). A main effect of Compatibility also emerged ($F(1,36)= 6.875$, $p=.013$), indicating slower responses during compatible trials (mean= 572 ms; SD= 56.51) than incompatible ones (mean= 566 ms; SD=52.92; Figure 4B). The Block Sequence factor did not reach significance ($F(1,36)= 2.994$, $p=.92$). No interaction was statistically significant (all ps >.05).

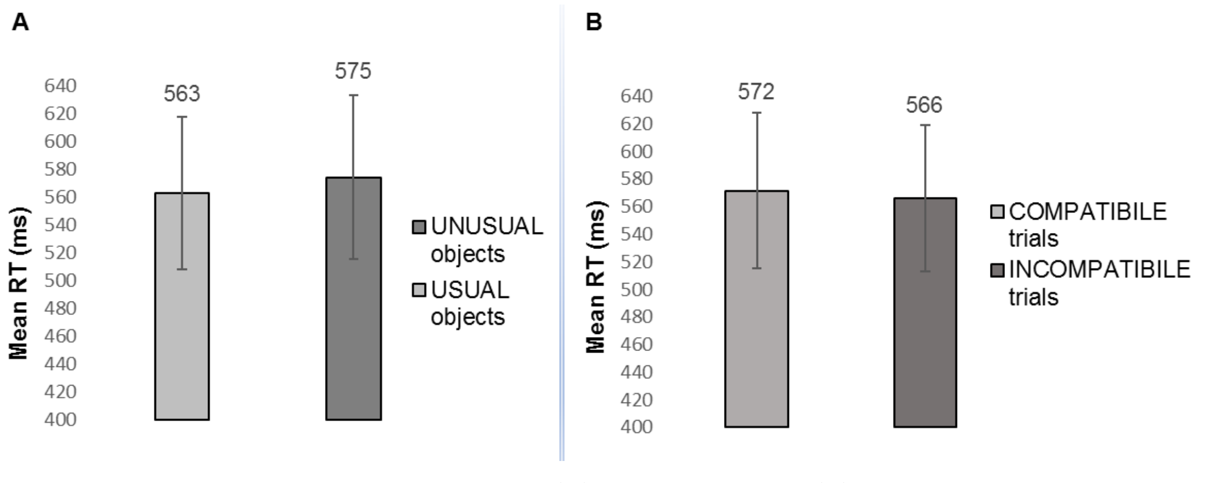


Figure 4. Mean RTs according to objects Type (**A**) and Compatibility (**B**) factors in Experiment 1. Error bars indicate standard deviation

2.1.3. Discussion

Results indicated that the structural variation does make the unusual objects less familiar to the extent to cause a disadvantage in RTs. However, irrespective of the type of the stimulus, we found an inverted compatibility effect, i.e. not congruent with the orientation of object's handle (as it occurs for the affordance effect). The result indicates that the functional part of the objects becomes the salient one while performing the (categorization) task for both types of object. Importantly, the lack of interaction between Type and Compatibility means that the functional part is still recognized in the unusual version of the objects. Such an inverted compatibility effect is in line with previous studies showing that the functional meaning of an object is inferred by the part which specifies its function (i.e. the head of the tool) and not by the graspable one (i.e. the handle; e.g. Belardinelli et al., 2016). This implies that, when perceiving objects, attention is primarily directed to the functional part of them (i.e. the most salient feature; e.g. Kourtis and Vingerhoets, 2015).

The significant effect of Type might reflect a simple familiarity effect (as unusual objects are recognizable but not prototypical) but might also be due to differences in processing the stable and variable features of the usual and unusual objects. Therefore, we ran a second experiment where we tried to emphasize both the action-execution component and the motor simulation one in order to clarify the temporal dynamics of the response phases (i.e. decision and execution) in facing with usual and unusual objects.

2.2. Experiment 2

This experiment aimed at highlighting the different phases of processing the functional and the structural features of the objects during the execution of a more complex motor response. Experiment 1 demonstrated that the functional part of the unusual object is still recognizable, but, since the motor representations associated to the typical use of the object would not be suitable anymore for grasping and using them, new motor plans, requiring different online visuomotor transformations, should be processed. Thus, the structural modification in the unusual objects should evidence a different involvement of the Function and the Structure systems during the response phases.

Participants were then required to perform a reach-and-grasp movement toward a device in order to accomplish the task demand. This manipulation was introduced to increase the role of motor simulation in processing the objects (see for example, Bub and Masson, 2010). The task demand was still to categorize the stimuli on the bases of their function (i.e. whether the seen object is used to feed oneself – to eat or to drink-or not), but participants were required to lift-off one of two lateralized keys to reach and squeeze a power-grip device (the same device used by Symes, Tucker, Ellis, Vainio and Ottoboni, 2008). In previous studies, object pictures disappeared just after the participants released the response key (e.g. Bub and Musson, 2010; Roest, Pecher, Naeije and Zeelenberg, 2016; Iani, Baroni, Pellicano and Nicoletti, 2011). However, in this experiment, object pictures remained on the screen until the squeezing of the device (i.e. during the entire movement execution) to prevent that the movement execution was performed without seeing the object and, therefore, that the trace concerning the visual structural modification of the unusual objects decayed. In this way, we avoided that the long-term, stored representations, based on the stable affordances processed by the Function system, prevailed over the short-term visual information which, instead, requires the contribution of the Structure system.

2.2.1. Method and Procedure

Participants

Forty-four, right-handed participants students of the University of Bologna (22 females; mean age=22.81; SD=2.18) participated in the experiment after giving their consent. All of them had normal or corrected-to-normal vision.

Ethics Statement

The experiment was approved in 2016 by the bioethical committee of the University of Bologna according to the Declaration of Helsinki.

Stimuli

The stimuli were the same as in Experiment 1.

Apparatus and procedure

Stimuli were presented on the same computer screen as in Experiment 1. The power grip device was centrally positioned in front of the screen. It was inserted in a wooden plank (40 cm long, 18.8 cm wide and 2.2 cm high), and it was 11 cm high with a diameter of 3 cm (Figure 5A). Finally, the keyboard was positioned in front of the device (Figure 5B). The hand-to-screen distance was approximately 20 cm and the viewing distance was approximately 60 cm. As in Experiment1, participants were required to perform a function-related task (i.e. to decide whether the object is used to feed oneself– to eat or to drink-or not). The usual and unusual objects were still presented in two separate blocks. The trial structure was the same, but participants had to respond by releasing one of the two lateralized keys ("x and ".") to reach and squeeze the device placed in front of them with the same responding hand. During the response phase, the stimulus remained on the screen until the device squeezing (i.e. for the duration of the movement). After the response, participants moved back to the starting position, and pressed both keys for the next trial to begin. The association between the correct yes/no response and the lateralized keys was counterbalanced between the participants. As in Experiment 1, an auditory signal informed the participants about their errors (i.e. when the wrong button was released). Overall 240 trials were presented (120 for each block), and ten practice trials, excluded from the analyses, preceded the experimental ones. As in Experiment 1, participants were allowed to have a short break every 40 trial.

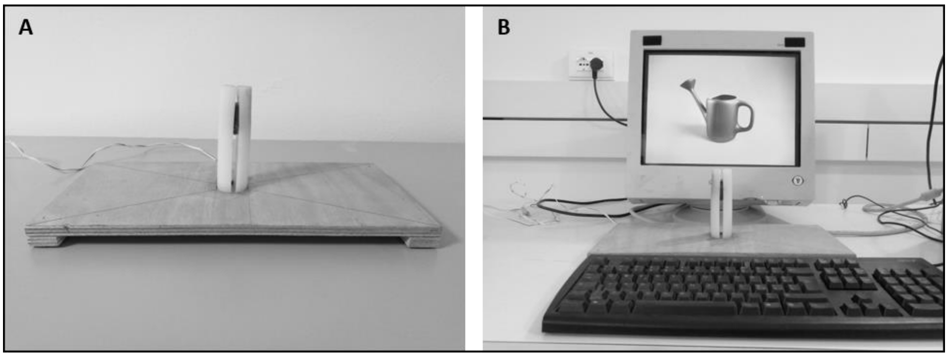


Figure 5. Power grip device **(A)** and Experimental setup **(B)** used in Experiment 2.

2.2.2. Results

As in Experiment 1, SPSS software (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp) was used to perform the analyses on the trials in which: i) the correct button had been released (i.e. if the wrong button was released, the following movement time was also excluded from the analyses); ii) both the lift-off and the movement time were not higher or lower than two standard deviations from the participant's mean. In this way, 9.47% of the total amount of trials was excluded. The two phases of the response were analyzed separately as in the previous literature in order to investigate any difference in the processing time of the two types of object (e.g. Bub and Masson, 2010; Roest et al., 2016): The releasing phase (from the stimulus onset to the release of the key, i.e. lift-off times, LTs) and the reaching phase (from the release of the key to the squeeze of the device, i.e. movement times, MTs). Two distinct repeated-measures ANOVAs were carried out on LTs and MTs on the same variables as in Experiment 1: i) Compatibility and ii) Type (Usual vs. Unusual Objects) as within-subjects factors; and iii) Block Sequence as between-subjects factor.

LTs

The main factors Compatibility ($F(1,42)=.654$, $p=.423$), Type ($F(1, 42)=.277$, $p=.602$), and Block Sequence ($F(1, 42)=.521$, $p=.474$) were not significant. No interactions reached significance (all Ps >.05) with the exception of Type x Block Sequence (F(1, 42)=6.283, p=.016). Paired-samples T-test comparisons showed that LTs for usual objects (mean= 588 ms; SD=51.16) were significantly slower than for unusual objects (mean=572 ms; SD=58,4) only when presented as first block (t(23) = 2.073, p=.05; Figure 6). The other comparisons were not significant (all Ps >.05).

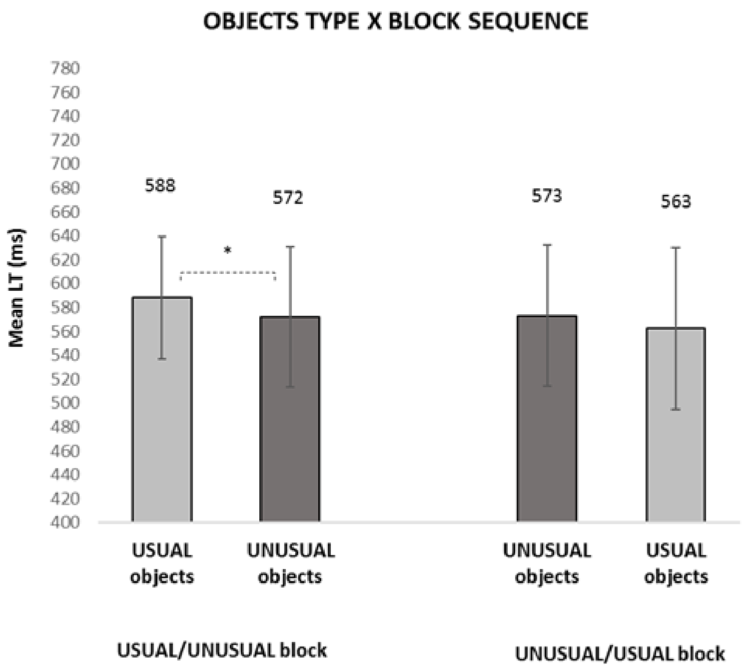


Figure 6. Mean Lift-off times- LTs comparing the objects type according to the block order of presentation in Experiment 2. Error bars indicate standard deviation. Statistically significant comparisons are shown.

MTs

No main effects emerged: Compatibility (F(1,42)=.005, p=.947), Type (F(1,42)=.517, p=.476), and Block Sequence (F(1,42)=.111, p =.741). No interaction reached the significance (all Ps >.05) but Type x Block Sequence (F(1,42)= 64.672, p<.0001): Overall, objects presented as second block elicited faster MTs. Paired-samples T-test comparisons showed that within the

Usual/Unusual Blocks, MTs were significantly faster for unusual objects (t(23)=4.831, p<.0001; mean=542 ms; SD=127.23) than for usual ones (mean=598 ms; SD=144.55), whereas within the Unusual/Usual Blocks MTs were significantly faster (t(19)=-7.19, p<.0001) for usual objects (mean=548 ms; SD=96.67) than for usual ones (mean=615 ms; SD=112.51). Moreover, independent-samples T-tests showed that unusual objects elicited significantly faster MTs (t(42)=-2.004, p= 0.05) when presented in the second block (mean: 615 ms; SD=112.51) than in the first one (mean:=542 ms; SD=127.23). However, responses to the usual objects showed no difference in relation to the order of presentation of blocks (t(42)=1.294, p= .2; Figure 7).

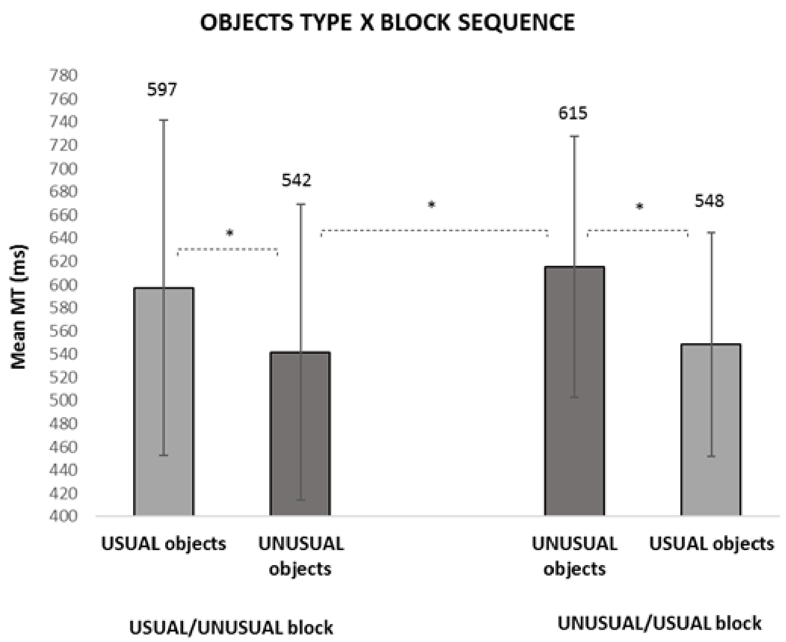


Figure 7. Mean Movement times - MTs**,** comparing the objects type according to the block order of presentation in Experiment 2. Error bars indicate standard deviation. Statistically significant comparisons are shown.

2.2.3. Discussion

The results from both LTs and MTs indicated that the order in which the two types of object were presented was able to affect object processing. This differently occurred according to the time of the response execution (lift-off vs. movement phase). Lift-off times were slower for usual objects only when presented first, while this did not occur when they were presented after the unusual objects. To note, in Experiment 1 reaction times were overall faster for usual objects. This different pattern could be ascribed to the addition of a real movement in responding to the stimuli, which induced a motor simulation process, able to highlight different processing mechanisms: Seeing usual objects first activated long-term, conceptual representations in a relative slow fashion, as already shown for example in Jax and Buxbaum (2010). On the contrary, seeing unusual objects in the first block, induced participants to use the visual, on-line analysis, faster than the deeper semantic processing: In this condition, when usual objects were subsequently presented, the visual, on-line analysis (i.e. the dorso-dorsal stream) was already triggered and ready to process also the usual objects (i.e. they were treated as they were "new" objects), too. Similar biasing effects due to block order have already been reported in both the motor (Tessari and Rumiati, 2004; Tessari, Bosanac and Rumiati, 2006; Tessari, Canessa, Ukmar and Rumiati, 2007; Cubelli et al., 2006) and language domains (Tabossi and Laghi, 1992; Ripamonti, Luzzatti, Zoccolotti and Traficante, 2017): In all these cases, when known stimuli were presented after the new ones they were treated as they were new as well, and a direct, non-semantic, process was used.

As regards MTs, results showed a significant Type X Block sequence interaction. If on the one hand they indicated that in general movements became faster in the second block, on the other one, they demonstrated the occurrence of a different elaboration mechanism according to the type of object. In particular, the responses toward usual objects were not affected by the order of presentation, as they did not significantly differ according to whether they were presented in the first or in the second block. On the contrary, the responses toward unusual objects were significantly faster when they were presented in the second block: They benefitted from the representations that have been elicited during the previous presentations of their usual form, since long-term, sensorimotor representations on their use were still active.

2.3. General discussion

This study aimed at extending findings on the contribution of functional and structural features during object processing. In particular, it has studied how the visual information dealing with the structure of the object matches the information stored in memory on object functionality. Functionally recognizable, but uncomfortable, versions of usual objects were matched with their usual counterparts. The unusual versions, requiring new actions/movements to be efficiently used, induced an ad-hoc peculiarity that modulated the recruitment of the Function and Structure systems.

In the experiments here presented, participants were asked to categorize objects according to a function-related property (i.e. whether the object is used to feed oneself or not) to ensure a deep elaboration of the stimuli (e.g. Borghi, 2004) and that both object identity and functional use were activated (Almeida et al., 2014).

In Experiment 1, object processing was investigated trough simple reaction times (button press responses). Results showed that for unusual objects a different processing load was required and that the demand of the semantic task was able to shift the attentional focus to the function-related parts of the object. In Experiment 2, a further motor component was added by asking to lift-off a key to reach and grasp a response device. Such experimental manipulation was chosen to better investigate the elaboration of functional and structural information in time. Indeed, previous studies demonstrated that lifting-off a key and performing a reach-to-grasp movement activate motor representations associated to the use-related actions that might not emerge in simple reaction times (Bub and Masson, 2010; Roest et al., 2016; Iani et al., 2011): Planning a functional grasp, i.e. the initial phase of object processing, activates the areas associated with tool use and the experiences related to their use (Przybylski and Kroliczak, 2016). Results from Experiment 2 indicated the contribution of both the elaboration of long-term representation (i.e. the ventro-dorsal stream) and the online visuomotor transformations (i.e. the dorso-dorsal stream) during the two response phases (i.e. decision and execution), which depended on the order in which the two object categories were presented and reflected the involvement of the Function and the Structure systems respectively.

In the following two paragraphs these findings will be discussed according to the presence of a compatibility effect (i.e. affordance effect) and to the different contribution of the two action systems involved in the object-directed actions.

On the affordance effect

The so-called affordance effect refers to an automatic activation manifesting itself in the form of a motor facilitation when the graspable part of the object (i.e. the handle) is oriented toward the same side of the responding hand (e.g. a right-oriented handle when responding with the right hand; Bub and Masson, 2010; Roest et al, 2016). The unusual version of the stimuli was used to investigate the effect of a variation of a stable affordance (such as object shape) on the onset of the affordance effect. Two main results emerged. First, participants responded faster when the handle was oriented towards the opposite side of the effector used to respond; Second, this reversed effect only emerged when the task required to press a button (Experiment 1), but no effect emerged when participants had to release a button to reach and squeeze a device (Experiment 2). Importantly, for both usual and unusual objects, participants' responses were compatible with the object functional, task-relevant part (e.g. the body of either the mug or the key, that are opposite to the handle), that is the part of the object which specifies and makes recognizable their use: The response selection relied on a mechanism which induced to focus attention on a part of the object, that is different from the handle, and prevented the typical affordance effect to emerge. Thus, according to the 2AS model (Buxbaum and Kalénine, 2010; Buxbaum, 2017) the Function system, based on object invariable features (i.e. stable affordances) and on stored representations of skilled actions associated with them, dominated the response selection and was not affected by the processing of the object altered structure (i.e. a variable affordance).

Although we detected slower RTs to unusual objects, we did not find any interaction between the Compatibility and Type of object factors. The delay in RTs for unusual objects may result from the mismatch between long-term representations of the objects and the visual information based on structure occurring while accessing to their functionality. However, this did not affect the strategy used to answer the task demand, which was the same for the two categories of objects (i.e. focusing on the functional part of the object in order to infer the purpose of its use).

Importantly, we did not observe any affordance or compatibility effect when participants released the button and performed a reach-to-grasp action (Experiment 2). Although other studies found the affordance effect only when response action required to lift-off a button, but not a key press (e.g., Bub and Masson, 2010; Cho and Proctor, 2010; 2011; Phillips and Ward, 2002; Roest et al., 2016), it is important to highlight the differences in the main task: They required participants to judge the object colour, whereas the object identity or functional meaning was task-irrelevant. Our results provide further evidence that the task demands are responsible for such an effect to emerge. As regards the MTs, the absence of the affordance effect is in line with previous literature, indicating that handle-to-hand compatibility effect arises during hand response selection and not during response execution (Bub and Masson, 2010; Roest et al., 2016).

On the contribution of the Function and the Structure systems in the response execution.

As reported above, in Experiment 2 a motor response component was added in order to emphasize the action execution component and motor simulation. The lift-off and reaching movement phases reflect different underlying mechanisms: The former is linked to action programming (e.g. the hand to use), whereas the latter is linked to action control and execution (Buxbaum, 2017). According to the dual route 2AS model (Buxbaum and Kalénine, 2010; 2AS+, Two Action Systems Plus; Buxbaum, 2017), the ventro-dorsal stream is supposed to be more involved in the former phase of the planned action, while the dorso-dorsal stream is supposed to be more involved in the latter one.

As concerns the first response phase, i.e. LTs, we found that when usual objects were presented before the unusual ones they caused significantly slower LTs. In the other condition, when usual objects were presented following the unusual ones, no difference was found. This occurred since the view of the usual objects in the first block activated an indirect strategy of processing, based on the access to the stored long-term motor representations of skilled use-related and experience-based actions (i.e. manipulation knowledge). Such an effect reflected the guidance of the Function system relying on the ventro-dorsal processing. Then, in the second block, the structural variation of the objects requires to plan new movements and the previous sensorimotor representations are no suitable anymore to accomplish the task. The processing mechanism swaps from the use of the indirect strategy to the adoption of one relying on the analysis of the visual structural features, during which predicted consequences of the motor commands are continuously compared with actual sensory information in order to correct any discrepancy, resulting in faster responses to accomplish the task (Sakreida et al., 2016; Buxbaum and Kalénine, 2010; Jax and Buxbaum, 2010). This represented the domain of the Structure system, relying on the dorso-dorsal processing. Such a change in the processing mechanisms did not occur when unusual objects were presented in the first block, most likely because the same rapid direct strategy used for unusual object elaboration is extended to the analysis of usual objects. A similar modulation of the processing mechanisms has also been evidenced during imitation of known and new gestures (e.g. Tessari and Cubelli, 2014; Tessari and Rumiati, 2004).

Our results are in line with a behavioral experiment from Jax and Buxbaum (2010) demonstrating that the Function and the Structure systems processing differently maintains information active while programming object-directed actions. They presented participants with two kinds of objects: Non-conflict objects required the same hand gesture to be moved or to be used (e.g. cup); while conflict objects required different hand movements according to the purpose of moving or of using them (e.g. calculator). The objects were intermixed in two separated counterbalanced blocks: In one block participants had to release a button and position the hand as they wanted to move the object (grasp-to-move task), in the other block participants had to release a button and position the hand as they wanted to use the object according to its function (grasp-to-use task). Besides a general advantage in initiation times (i.e. lift-off times) for non-conflict objects, results showed increased initiation times for conflict objects only when the grasp-to-use task preceded the grasp-to-move task. Such a pattern of initiation times indicates that the information activated for processing the objects according to their use, was still active after several minutes and interfered with the following grasp-to-move task. This did not occur when the order of tasks presentation was the opposite, indicating that information processed to move the object rapidly decayed. More recently, Lee and colleagues (Lee et al., 2018) reported results in line with the 2AS model in an event-related potentials (ERPs) study: They demonstrated that, according to the intended grasp-to-move or grasp-to-use action, the relevant object's features activated information related to actions differently in time: the early visual, online processing was followed by the late semantic counterpart.

As regard MTs, in general MTs for the objects presented in the second block were faster than those of objects presented in the first one, and this result can reflect a mere learning effect, due to participant habituation to the task as, in repeatedly executing the response movement, they have become faster and faster. More interestingly, MTs were also influenced by both object type and order of blocks presentation: MTs for unusual objects presented in the first block were significantly slower than MTs for those presented in the second block, i.e. after the usual objects. This result is interpreted as a main recruitment of the Structure system (i.e. the dorso-dorsal stream) during the motor, online control, which is evident when the unusual objects cannot rely on a previous activation of the Function system (i.e. the ventro-dorsal stream): Only in this case the dorso-dorsal stream faces with a new object structure without having a background activation of the use-related motor representations referring to the similar usual objects. Indeed, as it has been shown that objects rapidly evoke bilateral representations of hand postures and that the parameters relating to the action continue to be defined online even after the beginning of the movement (Bub and Masson, 2010), the increment in MTs according to the order of block presentation indicates that the specification of movements mainly recruited the Structure system when unusual objects must be processed. It is important to note that no difference was found in the MT with the usual objects, confirming that it is not necessary to recalibrate the movements related to the action for this type of objects and the long-term motor representations, elicited in the Function system, still adapt well with the observed stimuli.

All together, these results highlight the distinct phases of the response in which the Structure system and the Function system are preferentially recruited.

Chapter 3

A kinematic investigation of the function-based and the structure-based object processing.

As extensively discussed in Chapter 1, stable affordances (which remain the same in all the contexts when interacting with the object) and variable affordances (which must be processed *ex novo* every time, as they strictly depend on the context; see Borghi and Riggio, 2009; 2015) are processed in two distinct anatomical networks (for a recent meta-analysis see Sakreida et al, 2016), located inside the dorsal stream for action (Rizolatti and Matelli, 2003; Binkofski and Buxbaum, 2013; Brandi et al., 2014; for a brief review see also Binkofski and Buccino, 2018): The ventro-dorsal stream, mainly involved in the processing of stable affordances, serves the associations between the object and the movement necessary to its manipulation, and stores them in the form of non-declarative sensorimotor representations based on previous motor experiences; The dorso-dorsal stream, mainly involved during the processing of variable affordances, is specialized on visuomotor transformation guiding on line processes of motor control and action adaptation, based on visual information, which is constantly updated. During the execution of daily actions, these two systems process in parallel the object and the cognitive system needs to constantly compare the motor activation of the two streams to select only the representation relevant for the individual purposes (e.g. Caligiore, Borghi, Parisi and Baldassarre, 2010; Buxabum and Kalénine, 2010).

Besides their different specializations, the dorsal streams seem to be characterized by a different processing timing. The ventro-dorsal stream is activated in a slower fashion and it is able to work on a greater load of information which is maintained active for a relatively long period of time (Borghi and Riggio, 2009). In contrast, the dorso-dorsal stream is rapidly activated, but it is more transient, with visual information rapidly decaying (Pisella et al., 2000; Rossetti, Revol, McIntosch, Pisella, Rode and Danckert, 2005). Evidence on this timing difference came primarily from a behavioural study. Jax and Buxbaum (2010) investigated the competition between grasp-to-use movements (i.e. movements programmed on the base of the functional use of the object) and grasp-to-move movements (i.e. movements programmed on the base of the structure of the object), using objects which require different grips according to the purpose of using or merely moving them. Results showed that use-related movements were able to affect move-related response times, indicating that the activation of the former ones still survived after several minutes. The absence of the opposite pattern (i.e. no influence of move-related gestures on the use-related ones) indicated that the source of information for programming move-related gestures rapidly decayed. As move-related and use-related gestures are supposed to be mediated by the dorso-dorsal and the ventro-dorsal stream respectively, this suggests that stable affordances rely on slow modalities of operations and variable affordances on fast operations (Jax and Buxbaum, 2010; Borghi and Riggio, 2015; Binkofski and Buccino; 2018).

Other studies demonstrated that structure-based and function-based actions elicit different temporal pattern of processing, especially through language understanding and action observation in both healthy subjects (Lee et al., 2012; 2018) and brain damaged patients (Myung et al., 2010; Lee et al., 2014). Anyway, to our knowledge, no study focused on the integration of information stemming from the different kind of affordances by investigating the involvement of the two dorsal streams at a kinematic level.

Previous investigations assessed that kinematics parameters of grasp vary according to the action to be executed after the object is grasped, considering also the end-goal besides the object structural geometry (Valyear et al., 2011; Armbrüster and Spijkers, 2006; Ansuini, Santello, Massaccesi and Castiello, 2006; Ansuini, Giosa, Turella, Altoè and Castiello, 2008). Valyear and colleagues (2011) demonstrated that grasping an object in order to use it caused a wider opening of the fingers in comparison to grasping an object in order to move it, regardless of the variation of the task setting, suggesting a robust difference in grasping depending on the task demand.

Moreover, it has been demonstrated that a specific action elicited by object properties is able to affect not only the motor preparation phase (i.e. reaction times), but also kinematics during action execution (Rounis, Polanen and Davare, 2018). Rounis and colleagues (2018) demonstrated that the presence of a handle on a cup caused a shorter maximal grip aperture (MGA, i.e. the maximal distance between the thumb and the index finger reached during the reaching phase) during a grasp-to-move action, in comparison to the absence of the handle, even if in both cases the task required to grasp the cup by the (identical) rim.

Even though these studies described the role played by the affordances in the kinematics of movement according to different task demands, there is no evidence about the contribution of function-related vs structure-related object properties when we plan and execute object-directed actions.

Considering that the neural mechanism underlying the transformation of objects' visual information into specific motor commands for manipulating them is affected by both visual guide and long-term representations (Begliomini, Caria, Grodd and Castiello, 2007), the aim of this study was to investigate how the processing of object properties guides motor planning and execution during reach-to-grasp movements at different levels of vision availability. As variable affordances are supposed to be processed by the dorso-dorsal stream via a visually guided analysis of the object structural (i.e. geometrical) properties, the availability of visual guidance was modulated by the use of shutting glasses, which were able to prevent participants vision at different time points, in order to affect motor plan and execution.

Previous literature extensively investigated the time course of the decay of visually-derived information about the internal representation of the object and the environment used to guide reaching and grasping movements in absence of the vision. It seems that a delay of 2 seconds between visual presentation and motor response is able to affect the online guidance, which rapidly decays (Goodale and Westwood, 2005; Westwood and Goodale, 2003). It has been proposed that, after this period, the movement turns in being based on stored perceptual representations activated by the ventral stream (Goodale and Westwood, 2005; Westwood and Goodale, 2003, Goodale, Jakobson and Keillor, 1994). In 1994, Goodale and colleagues showed kinematic differences between grasping movements pantomimed after a delay of 2 seconds from the view of the object and grasping movements pantomimed in real time, suggesting that in the former case the movements were based on long term stored information. Evidence of kinematics changes of hand's movements in condition of prevented vision during the grasping of an object (e.g. Heath, Rival and Neely, 2006; Hesse and Franz, 2010; Hu and Goodale, 2000) generally demonstrated that delayed movements are typically less accurate, slower and with a larger grip aperture (Hesse and Franz, 2010; Schettino, Adamovich and Poizner, 2003). Moreover, the effect of object-directed delayed actions has been demonstrated to affect also gaze patterns (e.g. Prime and Marotta, 2013) and motor evoked potentials (MEPs) facilitation (e.g. Prabhu, Lemon and Haggard, 2007). Thus, on one hand the literature demonstrated that the information processed by the visually-guided analysis rapidly decays, on the other hand, sensorimotor representations of functional use-related action features, that are activated during the planning phase by the ventro-dorsal stream (Johnson-Frey, 2005; McDowell et al., 2018), maintain active the "desired goal-state" to achieve the action for a longer period of time, on the base of stable, core object features (Sakreida et al., 2016, Buxbaum, 2017). Tunik and colleagues (2008a) demonstrated that Transcranial Magnetic Stimulation (TMS) over a crucial area of the ventro-dorsal stream (i.e. the Supramarginal Gyrus, SMG) was able to slow down the planning phase of object-directed actions. Interestingly, kinematic parameters were not affected by the stimulation, and the effect was observed only for object-directed actions (and not for control actions which did not imply any interaction with objects), suggesting that SMG may play a role in planning hand movements to use an object in a purposeful way.

As said above, the aim of our study was to investigate how objects properties (i.e. stable and variable affordances) are processed in time and how the information they convey affect object-directed actions. To do so, we carried out both a quantitative analysis of kinematic parameters and a qualitative analysis of movement accuracy (on video recorded participants performances). We adopted three main experimental manipulations in order to modulate the role of the object properties. First, the actions were directed toward two object types: usual (i.e. normal) and unusual (i.e. structurally modified) objects. The unusual objects were still clearly recognizable, but different movements had to be programmed in order to use them according to their function, as their structure was altered. This manipulation was thought to create a mismatch between visually-guided information conveyed by their structure and stored experience-based information about how to functionally manipulate them. Second, we asked participants to reach and grasp objects and demonstrate their use. This ensured the access to object identity and therefore the activation of stored sensorimotor representations about object manipulation (i.e. manipulation knowledge; Buxbaum and Kalénine, 2010; see also Almeida et al., 2014). In this way, the movements were programmed on the base of their function and not of their structure (see Rosenbaum, Chapman, Weigelt, Weiss and van der Wel, 2012). Third, grasp-to-use actions were performed in three different conditions in which the availability of visual information was progressively reduced. In the first condition participants could see the object during all the duration of the execution (i.e. baseline). In the second condition participant could see the objects for 500 ms and, immediately after, grasp them without seeing them (immediate grasp without vision). In the third one, participants could see the objects for 500 ms as well, but they had to grasp them after a delay of 3 seconds in which their vision remained occluded (delayed grasp without vision). While in the second condition the onset of the movement can still partially rely on visual information (albeit decaying), in the last condition the delay of three seconds was adopted to cause the decay of the visual information, leading the grasp-to-use action to be performed on the base of long-term sensorimotor representations. Additionally, the condition 2 was expected to elicit the higher level of conflict, because of the need to integrate the identity-related function of the object with its new (never-experienced) structure in a very brief time window (i.e. 500 msec). that is a stable feature (i.e. object shape) turned into a new (i.e. variable) one to be processed.

We measured both transport (i.e. reaction and movement times) and grasp (i.e. maximal grip aperture) kinematics (Hesse and Franz, 2010; Valyear eta al., 2012; Rounis et al., 2018). We also analysed the occurrence of the cases in which, due to the experimental manipulations, participants explored the space close to the object to find its exact location. Moreover, the analysis of errors related to both the motor execution and the functional processing of objects (see Method) was also included in the investigation.

In this way it was possible to observe how stable and variable affordances were processed and integrated in condition of degraded visual information during different movement phases: before grasping of the object (i.e. planning and reaching phases) by the mean of kinematic parameters (i.e., RTs, MTs, MGA) and exploration errors, and after the grasping (i.e. the execution of a function-related movement) by the mean of the qualitative analysis of errors.

3.1. Method and Procedure

Participants

Forty-six right-handed volunteers (5 female, mean age=23,56, SD=2,04), enrolled among students at the University of Bologna, participated in the experiment after giving their consent. All of them had normal or corrected-to-normal vision.

Ethics Statement

The experiment was approved by the bioethical committee of the University of Bologna according to the Declaration of Helsinki.

Stimuli

Six usual objects and their unusual versions were used (Figure 8). The ratio behind the choice of these stimuli was the same of that of Study 1.

Figure 8. Stimuli: couples of Usual objects (on the left) with their corresponding Unusual version (on the right).

Experimental setup

Participants performed the task sitting at a table and wearing PLATO Visual Occlusion Spectacles controlled by E Prime 2.0. To start each trial, with their right hand they had to press a start button, positioned 20 cm to their right side and controlled by E Prime 2.0. Objects to be grasped were positioned on the table, in front of them. In order to make the grasping gesture comfortable, all the objects but the mug were placed on a small support which was changed by the experimenter according to the object to be presented and stuck on a wooden squared base (40 x 34 cm) positioned 13 cm ahead from the edge of the table. In this way, objects were slightly lifted from the base and participants could easily grasp them. The mug was placed directly on the wooden base, which was identical for all the objects. Moreover, objects were presented with the handle orienting 45° to the right, in order to facilitate the grasping gesture with the right hand. The distance between the participant’s hand and the object was the same for both the usual and unusual version of each object.

A video camera was placed in front of the table, pointing toward the participants, to record their performances for the subsequent qualitative analysis of errors.

Kinematic recording

Kinematics of the participants’ right hand were tracked using a 3D-optoelectronic Smart-D System (Bioengineering Technology & Systems, BTS). Four infrared reflective markers (10 mm in diameter) were placed on each participant hand: one on the thumb nail, one on the index finger nail, and two on the right and left side of the wrist, at the level of the head of the ulna. They were used to measure transport and grip components of the movement. A fifth marker was positioned on the object and used to detect the point in time in which it was reached and moved. Four infrared video cameras (sampling rate 120 Hz) were placed at the four angles of the table. The calibration of the cameras position, focus and brightness was carried out for each participant.

Procedure

Participants were required to grasp and demonstrate the use of the object placed in front of them with their right hand. At the beginning of each trial, the shutting glasses were opaque (i.e. vision was prevented) and the experimenter placed the object target on the table. After the go signal provided by the experimenter, participants had to press the strat button until they heard an auditory cue (1000 Hz of frequency and 1000 msec of duration). The button press was triggered to the BTS System and the kinematic recording started. After 2 seconds from the button press, the glasses became transparent for 500 msec allowing the view of the object, and the auditory cue was delivered to provide the signal to begin the grasp-to-use movement. The sequence between the opening of the glasses and the auditory signal defined three experimental conditions (Fig 9A).

- In the Condition 1, after 500 ms of object vision the glasses remained transparent and participants heard the auditory signal. In this way, they could grasp the object immediately and under the guidance of vision (i.e. without any interfering manipulation);

- In the Condition 2, after 500 ms of object vision the glasses became opaque and simultaneously participants heard the auditory signal. In this way, they had to grasp the object immediately, but in the absence of vision;

- In the Condition 3, after 500 ms of object vision the glasses became opaque and the auditory signal was delivered after 3 seconds. During this delay and after the auditory signal, vision was prevented (i.e. the glasses remained opaque). In this way participants had to perform a delayed action in the absence of vision. The delay of 3 seconds was chosen to ensure the decay of visual information (Goodale and Westwood, 1995; Westwood and Goodale, 2003; Figure 9B).

Participants were encouraged to perform the action quickly but at a comfortable speed. After demonstrating the use of the object, participants were required to lay the object on the table, to come back in the start position and press again the button. Kinematics recording stopped automatically after 12 seconds in the Condition 1 and 2, and after 15 seconds in the Condition 3. This time ensured that the reaching and grasping phase (i.e. the movement phases of interest) was recorded. The experimenter saved the data of the current trial and set the recording of the following one.

Before the beginning of the experimental trials, participants performed five practice trials consisting in grasping and lifting a sponge ball, in order to familiarize with the temporal dynamics of the experimental condition.

Usual and unusual objects were presented once and mixed together. The order of presentation was randomized across participants. Each participant was assigned to one single experimental condition, in a between-subjects experimental design.

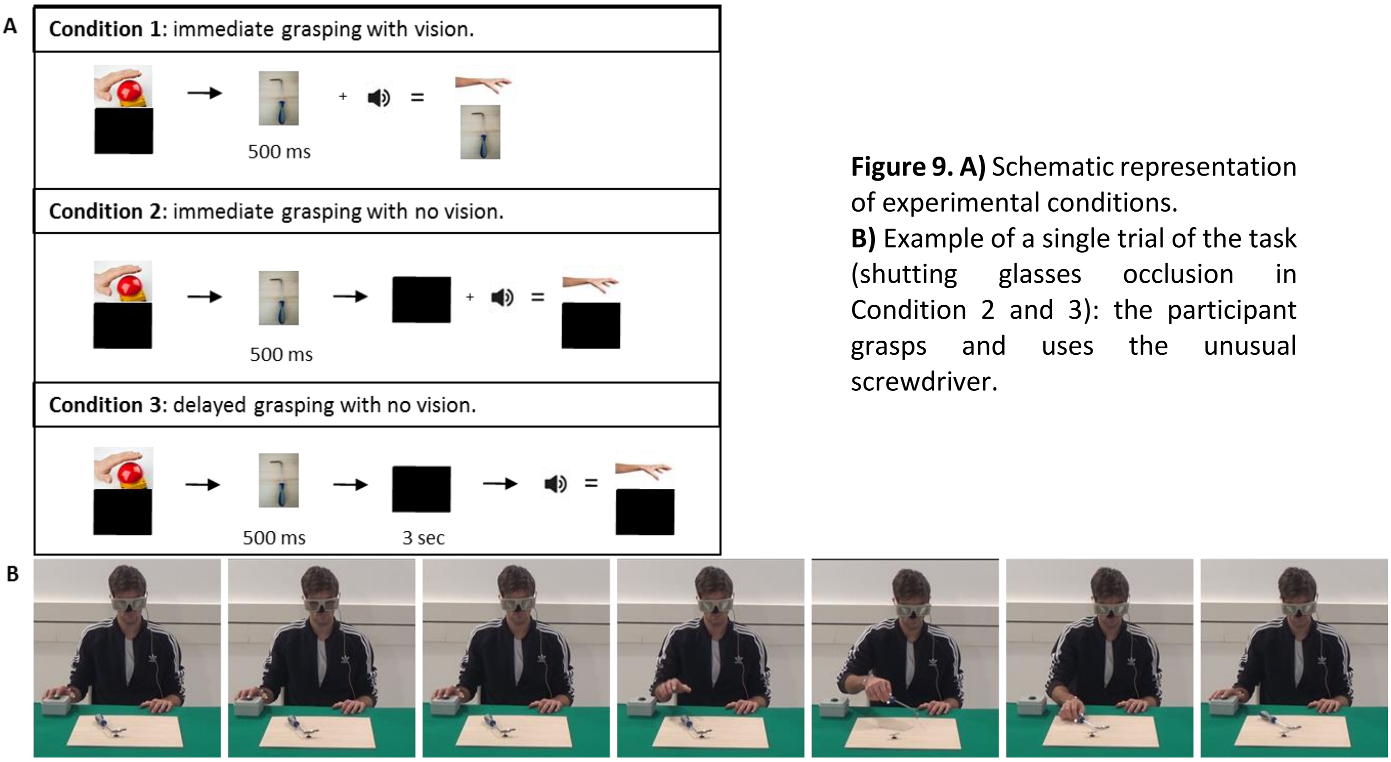


Figure 9. A) Schematic representation of experimental conditions. **B)** Example of a single trial of the task (shutting glasses occlusion in Condition 2 and 3): the participant grasps and uses the unusual screwdriver.

3.2. Kinematic data analysis

After collecting the data, each trial was checked. First, the correct identification and the labelling of the markers was carried out. After that, by using the SMART-D Tracker software package (BTS) 3-D reconstructions of the marker position as a function of time were obtained. Then, kinematics parameters were analysed and extrapolated using custom-written scripts in MATLAB (MathWorks). Index and thumb tracks presenting gaps more than 5 frames were excluded from the analyses. For gaps smaller (or equal) than 5 frames, we interpolated the data position using the piecewise polynomial form of the cubic spline function (de Boor 1978).

Moreover, the mug and the key were excluded from the kinematic analysis. The former because it was often grasped from the body eliminating the difference between usual and unusual version of the object. Additionally, the amount of available trials did not allow to analyse separately the two grasps according to the object type. Similarly, the key was excluded because the size of the graspable part between the usual and the unusual version was different. Finally, we excluded the trials in which: participants did not recognize the object (because the kinematics of such trials cannot represent the cognitive processing of the objects, which is the main purpose of our study); the system crashed or the participants released the button before the auditory (starting) cue (8,52%).

We focused on three kinematic parameters: Reaction Times (RTs), Movement Times (MTs) and Maximum Grip Aperture (MGA). RTs corresponded to the time in which participants released the button (i.e. movement onset). RTs faster than 200 ms and slower than 1500 ms were excluded from the analysis (1,24%). MTs were defined as the time between the movement onset and the reaching of the object. We considered the movement completed when the object reached a velocity of 30 mm/sec. The trials excluded from the RTs, were also excluded for MTs; in addition, we excluded MTs slower than 3000 ms (0,46 %) and the trials in which the quality of the track did not allow the extrapolation of the parameters (46,7 %). MGA was defined as the maximum distance between the thumb and the index finger during the reaching phase (i.e. during the movement time). The same trials considered for MTs were also considered for MGA.

For each of these parameters, we ran a repeated-measures ANOVA, considering the Experimental Condition (1,2 and 3) as between-subject factor, and the Type of Object (i.e. Usual vs Unusual object) as within-subject factor.

3.3. Qualitative analyses

The video-recorded performances were used to detect the occurrence of two kinds of errors. *Movement-related* errors included (i) the cases in which the participant did not grasp the object in the optimal way, although the use-related movement was well executed and the object correctly oriented (i.e. grasp errors) and (ii) the cases in which they correctly grasped the object, but the movement was executed in a wrong orientation. *Function-related* errors, instead, were related to the meaning ascribed to the objects. This category included (i) the cases in which an unusual object was used as the respective usual one, neglecting the structural variation (i.e. regularization), and

(ii) the cases in which an object was used as another meaningful object not included in the sample (i.e. lexicalization). Moreover, we included in this analysis the trials in which participants did not recognize the object.

At last we included in the analysis also the cases in the conditions 2 and 3, in which, due to the prevented vision, participants tended to explore the space close to the object to exactly find its location and the position of the graspable part (*spatial* explorations).

In these analyses we considered the entire set of objects.

3.4. Kinematic results

RTs

From this analysis neither a significant main effect of Type ($F_{(41,1)}$= 1,88; p= .178;) nor of Condition ($F_{(41, 2)}$= 2,55; p= .09) emerged. No interaction was significant (all ps > .05).

MTs

A significant effect of Condition emerged ($F_{(39, 2)}$= 7,99, p= .001). Independent-samples t-tests revealed shorter MTs in condition 1 (mean= 762 ms; SD= 96,74) compared to both conditions 2 (mean= 877 ms; SD= 96,74; $t_{(52)}$ = -3,368 ;p= .001) and 3 (mean=1015 ms; SD= 243,42; $t_{(38,46)}$= -5,273; p< .001). Moreover, MTs in condition 2 were faster than in condition 3 ($t_{(54)}$ = -2,506 ;p= .01; Figure 10A). The effect of Type did not reach the significance ($F_{(39, 1)}$= 2,99, p= .09) and there were not significant interactions (all Ps> .05).

MGA

A main effect of Type emerged ($F_{(1,39)}$= 5,368, p<.026). Paired-samples t-tests revealed a significant smaller MGA for Unusual objects (mean= 96,99 mm; SD= 8,92) compared to Usual objects (mean= 94,28 mm; SD= 6,96; $t_{(41)}$ = 4,195 ; p< .001). A significant interaction Type X Condition also emerged ($F_{(2, 39)}$= 4,349, p= .02). Paired-sampled t-tests revealed that in condition 3 MGA was greater for Usual objects (mean= 101,8 mm; SD=12,75) than for Unusual objects (mean= 96,41 mm; SD= 7,54; $t_{(14)}$ = 3,06; p= .008). Moreover, independent-samples t-tests showed that for Usual objects MGA in condition 3 (mean= 101,8 mm; SD=12,75) was greater than in condition 1 (mean= 93,11 mm; SD=; $t_{(27)}$ = -2,248; p= .03; Figure 10B). No other effect or interaction were significant (all Ps> .05).

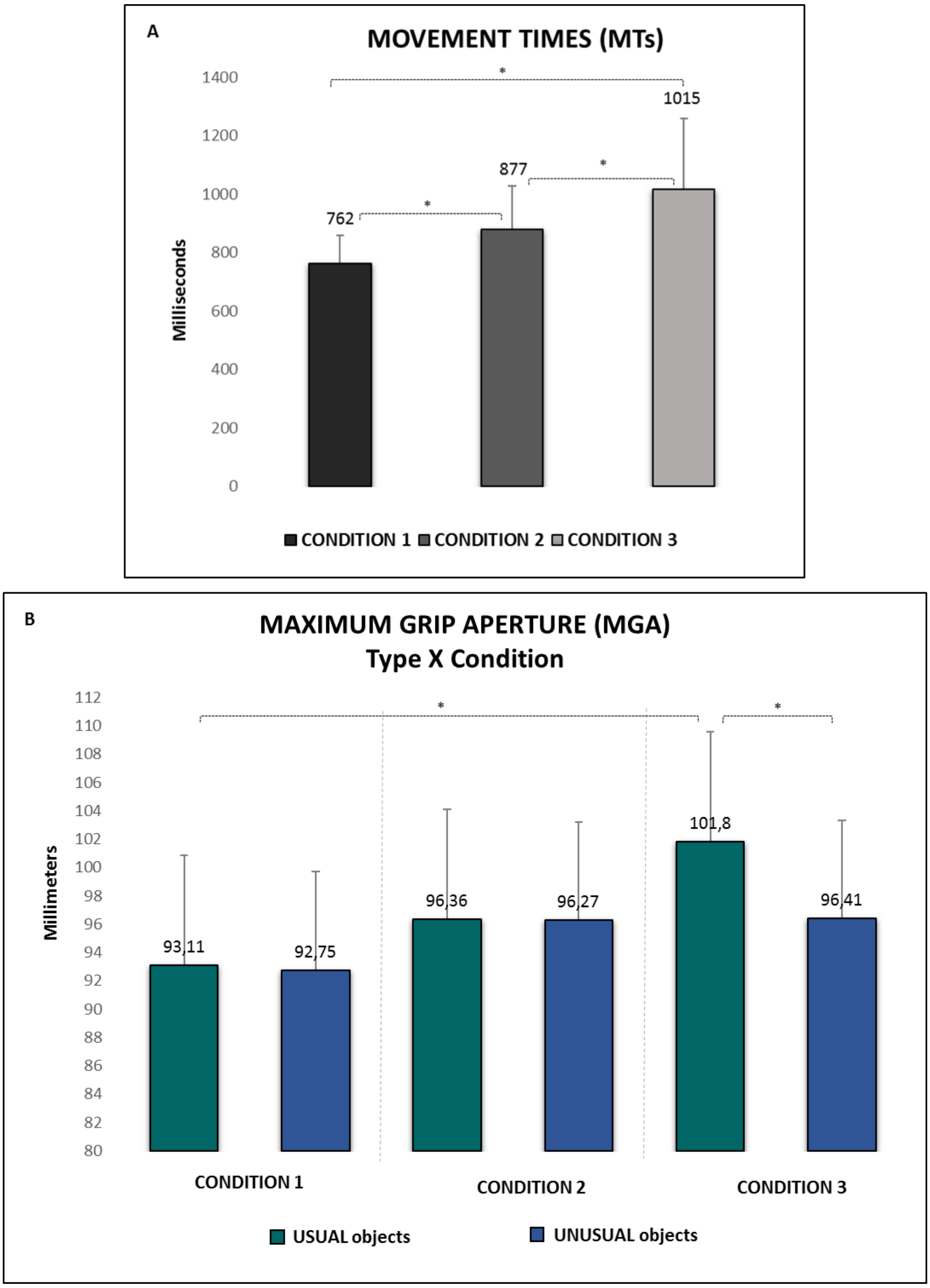


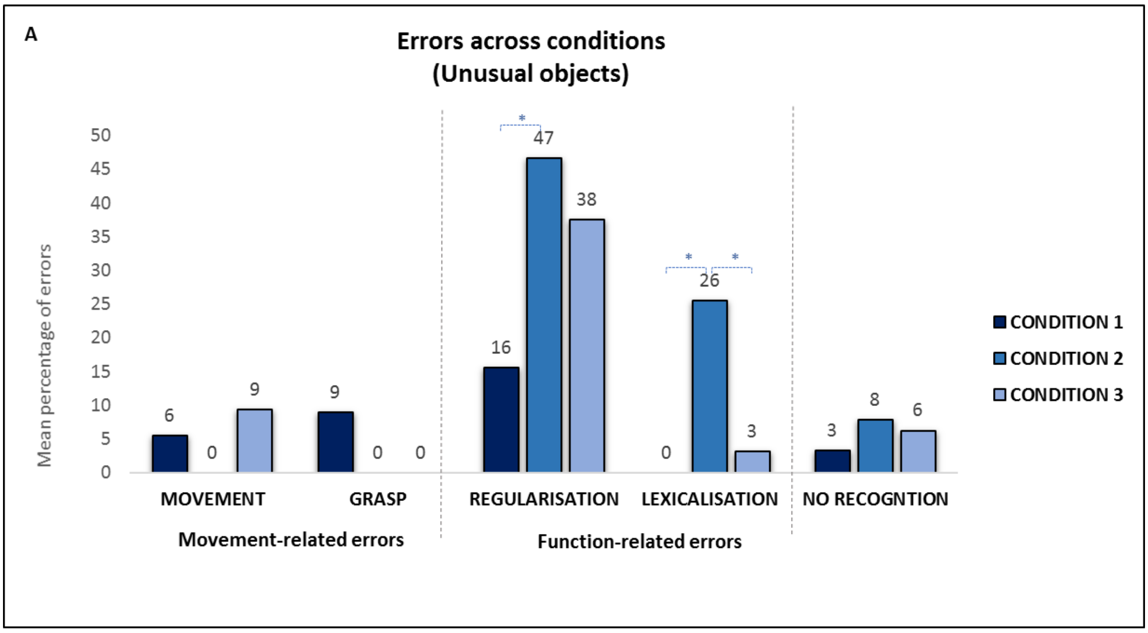
Figure 10. (A) Mean movement times (MTs) in the three experimental conditions. It indicates the time from movement onset to the contact with objects. **(B)** Mean Max Grip Aperture (MGA) in the three experimental conditions. It indicates the maximum distance between the index finger and the thumb during the reaching phase. Error bars indicate standard deviation. Statistically significant comparisons are shown.

3.5. Qualitative results

For the qualitative analysis, we asked two independent judges to detect the occurrences of errors and explorations. Cohen's k was run to determine the level of the agreement between their evaluations and it showed a substantial agreement (Altman, 1991) for both errors ($k= .81$; $p < .001$) and explorations ($k= .77$, $p < .001$).

The error analysis focused only on errors committed with unusual objects (N=44) and neglected the single error committed with usual objects. This clearly implies a main effect of the type of Object (Wilcoxon signed-rank test: $z= -5,855$, $p<.000$). For each error type, Mann-Whitney U tests were performed on the subjects' percentage of errors (Fig. 8A). This analysis showed that only Function-related errors emerged and occurred more often in condition 2: Regularizations occurred more often in condition 2 compared than in condition 1 ($U=68$, $z =- 2,05$, $p=.04$); and lexicalizations occurred more often in condition 2 than on both conditions 1 ($U=75$, $z =-2.39$, $p=.02$) and 3 ($U=86.5$, $z =-1.92$, $p=.05$; Fig 11A). The occurrence of the other errors did not differ across the conditions (all Ps >.05). As regards *spatial* explorations, Wilcoxon signed-rank tests showed that they were more frequent with Unusual than Usual ones ($Z = -2,184$; $p= .03$).

Moreover, Mann-Whitney U tests indicated that explorations occurred more frequently in condition 3 than in condition 2 ($U= 255$ $z = -3,327$, $p= .001$) for both Usual ($U= 62$ $z = -2,454$, $p= .01$) and Unusual ($U= 66$ $z = -2,262$, $p= .02$) objects (Fig 11B).



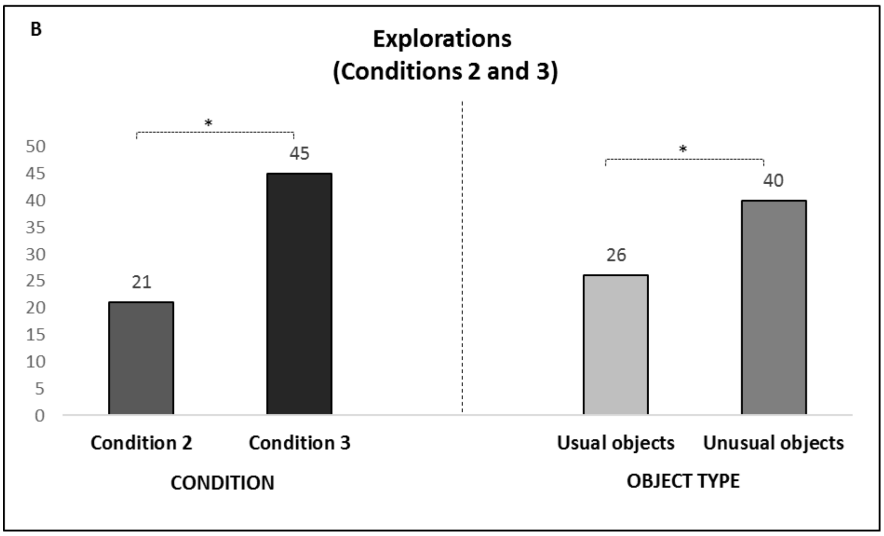


Figure 11. (A) Mean percentage of errors. Only errors committed with unusual objects were considered. **(B)** Number of *spatial* explorations in conditions 2 and 3 (no explorations occurred in condition 1).

3.6. Discussion

The study aimed at investigating the contribution of stable and variable affordances, when an action directed to the use of the object is required. The task demand elicited a deeper object processing based on the functional properties (Jax and Buxbaum, 2010; Valyear et al., 2011) and, therefore, the long-lasting activation of the ventro-dorsal stream (Binkofski and Buxbaum, 2013). As variable affordances, instead, are processed in the dorso-dorsal stream (Binkofski and Buxbaum, 2013; Borghi e Riggio, 2015), they are supposed to rapidly decay (within 2 seconds) when visual guidance is prevented (Goodale, Kròliczak and Westwood, 2005; Westwood and Goodale, 2003).

Therefore, we modulated the visual availability across the experimental conditions, leading them to generate different levels of interference during the parallel object processing by the two dorsal streams. The absence of any visual prevention in Condition 1 made it a baseline condition, in which the two dorsal streams could best cooperate and the information they processed could be integrated, modulating the weight of the streams according to the task demand. Condition 2 (i.e. a middle-way condition) implied a rapid integration of structural and functional object properties, generating the higher conflict between the two streams, due to the temporal constraints and with the information on the variable affordance, elaborated along the dorso-dorsal stream, decaying during the movement execution. At last, Condition 3 implied a decaying of on-line visual information, preventing participants to adapt their movement according to the object visual features, and with the stored experience-based sensorimotor representations about object manipulation driving the action.

Importantly, while previous kinematic studies presented tools (e.g. Valyear et al., 2012; Rounis et al., 2018) or meaningless objects (i.e. geometrical shape; e.g. Schettino et al., 2003; Franz and Hesse 2010), this time a new category of objects, which were meaningful in terms of function, but whose procedural manipulation knowledge was not stored through sensorimotor representations, were used. Therefore, the use of unusual objects, besides the usual ones, was thought to modulate the weight of the affordances across the experimental conditions. Unusual objects require to rely more on variable affordances than usual objects, and to recruit the dorso-dorsal stream to a greater extent. In particular, variable affordances were supposed to affect "use" actions in condition in which vision was prevented (i.e. condition 2 and 3), because of the mismatch between the information conveyed by the visually guided analysis and that conveyed by long-term, sensorimotor representations about how to purposefully manipulate them.

Overall, results suggested that the prevention of the vision and the object features differently affected the action during the different phases of movement planning and execution. First, although not emerging in the RTs, the modulation on the planning phase emerged from the analysis of the MGA, which varied in the condition of delayed actions, according to the object type. Secondly, the reaching phase was clearly affected by the visuo-spatial decay, as observed in the MTs, and as also confirmed by the *spatial* explorations. Finally, *function-related* errors confirmed that in the condition 2 the greatest interference between variable and stable features occurred and was clear in the last phase of action execution, that is the movement associated to the use of the object.

As regards RTs, we did not observe any effect. In a previous study, Hesse and Franz (2010) asked participants to grasp and move some geometrical blocks after a preview of 1000 ms in similar conditions of visual prevention. Also, their results did not show any difference in RTs. It might be that participants internalized the temporal sequence of a trial, knowing in advance the exact time in which they would have heard go-signal and, therefore, avoiding any effect to emerge. Indeed, the sequence between the button press and the auditory cue was fixed for all the trials and allowed the participants to merely learn it.

MTs pattern of results, instead, indicated that movements became slower and slower as the delay between the view of the object and the reaching movement (in condition of prevented vision) increased. This suggested that the prevention of vision caused the decay of spatial information and led to an increase of MTs, according to previous literature (Hu, Eagleson and Goodale, 1999; Jacobson and Goodale, 1991; Hesse and Franz, 2010; Schettino et al., 2003).

MGA showed patterns varying also on the base of the object type. The fact that MGA, among the other kinematic parameters, was affected by both the condition and the object type is not surprising. MGA has been demonstrated to be affected by a rapid decay of the visuomotor information (Westwood, McEachern and Roy, 2001; Franz and Hesse, 2010). Moreover, MGA is also considered the main kinematic landmark of grasping, which, being independent of the exact dimensions of the object, is thought to be an index of the influence of perception on action (Franz and Hesse, 2010). Our results indicated that MGA is bigger for Usual objects than for Unusual ones. Even if such an evidence could seem counterintuitive, it states that the grasping of the two kinds of objects differently recruited the two dorsal streams and, therefore, that variable and stable affordances were differently processed. Indeed, according to previous studies (Bub et al., 2008; Jax and Buxbaum, 2010; Buxbaum and Kalénine, 2010; Bub et al., 2018; Valyear, 2011), object processing is different in relation to the purpose of using or moving the object. It has been demonstrated that processing objects with the purpose of using them relies on the activation of the ventro-dorsal stream, while grasping the objects to move them mainly relies on the visually guided on-line processing by the dorso-dorsal stream (Buxbaum and Binkofski, 2013; Binkofski and Buccino, 2018; Kourtis et. al., 2018). Therefore, the two streams have been referred as the Use and the Grasp System respectively, with the former relying on the stable affordances and the latter relying on the variable ones (Borghi and Riggio, 2015; Buxbaum and Kalénine, 2010; Binkofski and Buxbaum, 2013).

In line with this literature, Valyear and colleagues (2011) asked participants to grasp familiar objects with the purpose of using or simply moving them. Importantly, the objects had the same handle. They found that MGA in grasp-to-use actions was bigger that in grasp-to move actions, confirming the different processing mechanisms highlighted by the task. A similar dissociation in the recruitment of Grasp and Use Systems might have been driven by the type of objects in our study (i.e. by the stimuli rather than by the task) and modulated by the structural variation of unusual objects. According to this interpretation, MGA of grasping gestures toward unusual objects were based on the processing of the exact metrics of the objects, therefore reflecting the on-line visually guided visuomotor transformation based on variable affordances (Binkofski and Buxbaum, 2013; Buccino and Binkofski, 2018; Sakreida et al., 2016; Kourtis et al., 2018). When grasping Usual objects, instead, stored representations about how to purposefully manipulate the object are activated, leading to a bigger MGA. This means that, being the task demand the same for all the stimuli, the differences in MGA between Usual and Unusual objects occurred because they elicited a different processing mechanism. Interestingly, results further showed that this difference of MGA emerged only in condition 3 and that for Usual objects MGA was significantly bigger in condition 3 than in condition 1, while MGA for Unusual objects did not vary across conditions. This MGA pattern highlighted two main results. First, the increment of MGA in Condition 3 for Usual objects indicated that the different role played by the stable and variable affordances between the two objects, as described above, was evident in the condition of maximum vision prevention, i.e. when the visual information was supposed to be decayed. Indeed, in condition 1 and 2, where it was still active (at least during the reaching phase), the Usual objects did not show any difference in MGA, because both visual information and sensorimotor representations were integrated and used to calibrate the movement. This is evident also from the absence of differences with MGA for Unusual objects in Condition 1 and 2. It is important to stress the fact that the handle of the objects was identical in their usual and the unusual versions.

Therefore, as the motor demand was the same for both object versions, it was not surprising that no differences emerged in the reaching phase, when all the information was available. Conversely, the fact that grasping Usual objects elicited a bigger MGA during the delayed action (i.e. condition 3) confirmed that the response was performed on the base of the ventro-dorsal activation, while the dorso-dorsal processing was less influential. The second result is that for Unusual objects, on the contrary, MGA did not vary across conditions and, consequently, it became smaller than MGA for Usual objects in condition 3. If on the one hand the absence of MGA variation for Unusual objects confirms that Usual and Unusual objects differently recruited the systems involved in object processing, on the other hand it also indicated that the structural, visually-guided information was still active at the end of the delay and suggested that the exact metrics of objects did not decay. The structurally modified appearance of unusual objects might have been considered a salient characteristic of the stimulus, and participants have likely focused their attention on a such unusual structure, allowing this information to be maintained active also during the delay. Indeed, there is some evidence for the maintenance of broad grasp-related motor plans during a temporal delay (e.g. Fiehler, Bannert, Bischoff, Blecker, Stark, Vaitl et al., 2011; Himmelbach, Nau, Zündorf, Erb, Perenin and Karnath, 2009; Singhal, Monaco, Kaufman and Culham, 2013). Therefore, the greater attention may be responsible of the maintenance of the visual properties of the object to be grasped.

However, besides MGA, both MTs and results about explorations suggested a decay of visual information. On the one hand, MTs slowed down from condition 1 to condition 3, and explorations increased from condition 2 to condition 3. Taken together these results demonstrated that spatial information of object location was affected by the progressive decrease of availability of visually guided information. To note, spatial information about object position is considered a further variable object property (i.e. in charge of the dordo-dorsal stream; Buxbaum and Kalénine, 2010; Binkofski and Buxbaum, 2013; Sakreida et al., 2016). Therefore, its decay very likely induced participants to explore the space close to the object and, in turn, this caused the increment in movement duration (i.e. MTs). Furthermore, the increment of explorations in condition 3 occurred with both Usual and Unusual objects, indicating that it did not depend on the object type.

Rather, the absence of MGA variation for Unusual objects together with the evidence of the decay of the spatial information seemed to suggest that reaching and grasping information are differently susceptible to decay. In line with this interpretation, literature showed that they rely on distinct neural circuits inside the dorso-dorsal stream (e.g. Binkofski et al., 1998; Binkosfki and Buxbaum, 2013).

Moreover, from the analyses of explorations also emerged that overall participants explored more when they had to grasp unusual object, compared to when they had to grasp usual objects. This would confirm that on-line visual processing by the dorso-dorsal stream was more recruited to interact with unusual objects and that, as dorso-dorsal stream invested substantial resources to process their structural properties, less cognitive resources could be used to maintain active the information about object location in space. This led to the increase of spatial exploration observed for usual objects compared to usual ones.

To sum up, kinematic results, together with the investigation on spatial explorations, revealed that usual and unusual objects were differently affected by the temporal delay, since, inducing to the predominance of stable and variable affordances respectively, they recruited the ventro-dorsal and the dorso-dorsal stream to a different extent. The greater recruitment of ventro-dorsal stream for usual objects was evident in the variation of MGA in condition 3, whereas the greater number of spatial explorations toward unusual objects, together with the absence of differences in the MGA, would explain a major involvement of the dorso-dorsal stream for those objects. One should keep in mind that participants were always required to use the objects, and that, therefore, the differences in the processing of the reaching and grasping were attributed to the cognitive systems recruited by the two object types.

While kinematic parameters and explorations revealed the influence of stable and variable affordances during the planning of the grasp (i.e. MGA) and the reaching phase (MTs), analysis on errors was used to investigate the latest phase of the response execution, i.e. the use of the objects. Overall, a robust result is that only unusual objects led to commit errors, as confirmed by the forty-four errors with unusual objects, in comparison to the only one observed with usual objects. The influence of object type confirmed that usual objects were recognized and correctly processed, while the structural variation of unusual ones caused a mismatch to be solved.

We focused on two kinds of errors: *Movement-related* and *function-related*. The former concerned the execution of the correct gesture according to the new, varied object structure (in relation to the grasp and the movement of the object); the latter concerned the meaning of the function conferred to the object. In this latter case we considered the cases in which the object was used as its usual equivalent (i.e. regularization), or as another (meaningful) object not included in the sample (i.e. lexicalization). Results indicated a predominance of only function-related errors in Condition 2, suggesting that movement parameters were always correctly adapted to grasp the objects, whereas the integration of stable and variable properties led to an interference to emerge based on the functional meaning of the objects. Indeed, we observed regularizations occurring in Condition 2 more often than in Condition 1 and lexicalizations occurring in Condition 2 more often than in both Conditions 1 and 3. Indeed, as said before, Condition 2 represents the context of the greatest interference between the two processing mechanisms. Errors pattern indicated that this interference could generate two outcomes.

In the case of a regularization, the manipulation knowledge about how to use the object prevailed, to the detriment of the visually guided analysis of the object structure. This resulted in a movement which represented the traditional use of the equivalent usual object. This error, as expected, occurred more in Condition 2 than in Condition 1, where the chance of integrating stable and variable object properties was higher. Instead, Condition 3 did not differ from Condition 1, likely due to the fact that accessing object identity avoided the structural information to decay. Thus, the structural information, being processed for the duration of delay, could be used to adapt the program of a new motor plan (as also demonstrated by the analysis of MGA for unusual objects). Indeed, previous studies investigating the time course of visually guided information used geometrical shapes as stimuli, that is they did not convey any associated semantic meaning (e.g. Goodale and Westwood, 1995; Westwood and Goodale, 2003; Hu et al., 1999; Jacobson and Goodale, 1991; Hesse and Franz, 2010; Schettino et al., 2003). Therefore, further investigations should be carried out to assess the influence of the semantic activation in condition of prevented vision.

In the case of a lexicalization, on the contrary, the visually guided analysis of object structure prevailed on the processing of the identity-related manipulation knowledge and movements were programmed in accordance to the perceived structure, even if referred to a meaningful object different from the presented stimulus. In this case, it is not surprising that such an error occurred more often in Condition 2 (compared to both conditions 1 and 3), i.e. where grasping actions had to be executed rapidly and in the absence of vision. Indeed, the greater number of occurrence of lexicalizations in Condition 2 reflected the predominance of variable affordances for unusual objects, but it also suggests that Condition 2 led to a slower activation of manipulation knowledge, based on the processing of stable affordances, to emerge, in comparison to the fast visually guided analysis based on the structural appearance of the objects. This interpretation would be in line with previous studies demonstrating the different time course of processing function-based vs structure-based object features (e.g. Jax and Buxbaum, 2010; Valyear et al., 2011; Lee et al., 2013; 2018; see also Guerard and Brodeur, 2015). However, while previous studies using real objects demonstrated a slower activation of function-based properties (Jax and Buxbaum, 2010; Valyear et al., 2011), in the condition 2 of this study, the combination of the structural variation of the unusual objects and the immediate grasping without vision was able to highlight also the rapid online visual analysis of object structure. As Bohg, Morales Asfour and Kragic (2014) noticed, grasps guided by the direct analysis of structural object properties occur when the task demands minimize the chance to rely on a stored "experience database", from which grasps are retrieved. Therefore, it is possible that asking to grasp unusual objects immediately after seeing them just for 500 ms led the participants to rely on such a direct fast analysis, driven by the visual objects features, rather than by their function. The occurrence of the lexicalizations (in which the function assigned to the objects was adapted on the base of their structure) could reflect this visually-driven mechanism.

At last, a further implication of the predominance of variable affordances, which led to lexicalizations, is that the visually guided analysis of the unusual objects induced participants to reason about the objects in order to find a purposeful way to use them according to their physical features. Osiurak and Badets (2016) defined this approach to object use as "technical reasoning", according to which the knowledge on the physical principles together with visual simulation enable tool use. However, while the authors claimed that this reasoning is sufficient to explain tool use (Osiurak and Badets, 2016), we agree with the idea that it may be one of the mechanisms on which tool used is based and that our brain would, more effortlessly, take advantage of a repertoire of known gestures, as stated by Buxbaum (2017).

Chapter 4

Interaction with unusual objects: a fMRI investigation of the factors modulating their processing within the vision-to-action systems.

Several functional Magnetic Resonance Imaging (fMRI) studies demonstrated that viewing objects elicits different brain activations in comparison to other non-manipulable categories of stimuli, such as animals or places (e.g. Chao and Martin, 2000; Mahon, Milleville, Negri, Rumiati, Caramazza, and Martin, 2007; Noppeney, Price, Penny, and Friston, 2005). The object-related activations concern a network that comprises, besides the medial fusiform gyrus and the posterior middle temporal gyrus, also the left superior parietal lobule (SPL), the intraparietal sulcus (IPS) and the inferior parietal lobule (IPL) (Lewis, 2006). While the former two temporal areas belong to the ventral stream (Milner and Goodale, 1995), the latter ones belong to two different pathways inside the dorsal stream (e.g. Rizzolatti and Matelli, 2003).

Indeed, as already reported, it has been recently demonstrated that object processing recruits two relatively distinct systems, underlying the planning and the execution of possible object-directed movements aiming at distinct goals and requiring different information to be executed (Buxbaum and Kalénine, 2010; Binkosfki and Buxbaum, 2013; Reynaud et al., 2016). At an anatomical level these two systems are supposed to constitute a further division (Rizzolatti and

Matelli, 2003; Binkofski and Buxbaum, 2013) of the original dorsal stream for action proposed by Milner and Goodale (1995): i) A dorso-dorsal stream, running from visual areas to the dorsal premotor cortex (dPMC), fundamentally involving the superior parietal lobule (SPL) and the intraparietal sulcus (IPS), responsible for object reaching and grasping according to the grasp they afford (i.e. Structure System; Buxbaum and Kalénine, 2010) and based on the visuomotor processing of objects' structural properties; ii) A ventro-dorsal stream, running from visual areas to ventral premotor cortex (vPMC), through the inferior parietal lobule (IPL), fundamentally involving the supramarginal gyrus (SMG), responsible for functional object-related actions based on long-term representations of skilled actions (i.e. Function System; Buxbaum and Kalénine, 2010). Previous fMRI studies have confirmed this dorsal subdivision and the different involvement of the two dorsal pathways according to the object features to be processed in both healthy participants (e.g. Hoeren, Kaller, Glauche, Vry, Rijntjes, Hamzei, and Weiller, 2013; Vingerhoets, 2008; Brandi et al., 2014; Reynaud, Lesourd, Navarro and Osiurak, 2016) and brain-damaged patients (e.g. Salazar-Lopez, Schwaiger and Hermsdörfer, 2016; see also Martin et al., 2016).

In relation to their different specializations, the ventro-dorsal and the dorso-dorsal streams are supposed to be recruited at a different extent during the processing of familiar or novel/unknown objects (Buxbaum, 2017).

In 2008, Vingerhoets carried out a study in which he compared neural activations related to familiar graspable objects and non-objects stimuli (e.g. scrambled pictures with a side larger than the other). Participants were asked to respond according to the orientation of the stimuli. His aim was to compare neural activations related to the processing of objects vs non-objects, that was expected to elicit a greater involvement of the left (IPL). Moreover, he compared familiar and unfamiliar tools, to investigate the neural effect of familiarity. Results suggested that only the objects activated the left-lateralized network devoted to tool-use and including posterior parietal, premotor frontal, and lateral posterior temporal areas. These results confirmed previous findings (Creem-Regehr and Lee, 2005) and suggested that the fact that tools, differently from the other stimuli, have a functionally-defined identity (i.e. a function-based specificity that relates to action) is responsible for the observed activation (Creem-Regehr and Lee, 2005). As regards the effect of familiarity, Vingerhoets found that, in comparison to unfamiliar objects, familiar objects activated at a greater extent the left supramarginal area extending to the left IPL, confirming that this region could store the representations of the position of the hand, necessary to purposefully use the object and formed on the base of previous experiences with the object (Buxbaum et al., 2003; 2005; 2006; Buxbaum and Kalénine, 2010; Buxbaum, 2017). Similarly, Salazar-Lopez and colleagues (2016) showed that the impairment in the use of objects in left brain-damaged patients was caused by lesions to IPL, especially in the SMG and the angular gyrus (AG).

Both in behavioural (e.g. Jax and Buxbaum, 2010; Valyear et al., 2011) and imaging studies (Valyear et al., 2012; Gallivan et al., 2013) it has been demonstrated that, besides the experience-based knowledge about object manipulation (Vingerhoets, 2008), also the task modulates the recruitment of the network devoted to tool use during the planning and execution phases. Brandi and colleagues (2014) carried out a fMRI study in which they asked participants to grasp familiar objects and neutral bar-shaped (i.e. meaningless) objects with the purpose of merely moving them or purposefully using them. On the one hand, results showed a dorso-dorsal role in monitoring the manipulation-related action for both types of the object, that is regardless of the prior knowledge about them. This mechanism involved the regions associated to object grasping (SPL, dorsal premotor area -dPM-, superior occipital gyrus -SOG-). On the other hand, a ventro-dorsal recruitment was observed in relation to the specific use of known (familiar) objects in the left SMG, postcentral gyrus and ventral premotor area (vPM). These clusters of activation are in line with the division presented by Binkofski and Buxbaum (2013), with the “grasp” network corresponding to the dorso-dorsal stream and the “function” network corresponding to the ventro-dorsal stream.

Thus, these studies confirmed the functional and anatomical definition of the two dorsal streams implicated during the interaction with the objects. As previously described, the specializations of the dorsal streams mirror the processing of distinct object properties, which are differently represented at a cognitive level and which are selectively used according to the task demand. These properties correspond to the stable (i.e. invariable) and variable (i.e. transient) affordances (Borghi and Riggio, 2009; 2015). A recent metanalysis demonstrated that stable affordances are mainly processed in the ventro-dorsal stream, while variable affordances are processed preferentially in the dorso-dorsal stream. Moreover, the two streams showed overlapping activations in the IPS, which is supposed to be a convergence area in which the information coming from the two dorsal streams is merged to be used for the action planning and execution (Sakreida et al., 2016).

While previous studies investigated the functional role of the two dorsal streams when people face with traditional or meaningless (i.e. neutral) objects (e.g. Vingerhoets, 2008; Brandi et al, 2014; Salazar-Lopez et al., 2016; Mahon et al., 2007; Noppeney et al., 2005), none has studied neural activations in condition of ambiguity between the information conveyed by the long-term representations about object use (processed by the ventro-dorsal stream) and the visually-guided processing by the dorso-dorsal stream. To this aim we performed a fMRI study using usual (i.e. traditional) objects and an unusual (i.e. structurally modified) version of them, which made them still fully recognizable, but their altered structure forced the observer to plan new, uncomfortable, grasp-to-use movements. The use of unusual objects is relevant in the light of the fact that their function is still evident (i.e. they are still meaningful objects), but the associated manipulative movements only refer to previous experiences with the traditional version of them (i.e. in these terms they could be considered unknown/unfamiliar objects). In this sense they should induce a greater load of processing, because a stable affordance (i.e. the shape) requires to be treated as a variable one, and therefore a greater recruitment of the on-line processing mechanism should be observed.

The neural structures recruited along the dorsal systems were investigated while usual and unusual objects were processed during a functional categorization task (*objects* task), aiming at assessing whether the structural variation of the unusual objects interferes with the computational processing of the way objects are manipulated to be used. Similarly to the task demand in Study 1, participants were required to judge whether the presented object could be used to eat / drink or not. Such a categorization task was supposed to require the access to the object (semantic) identity, which, in turn activates the representations about how to purposefully manipulate it (Almeida et al., 2013)

Moreover, another task, in which participants had to categorize two geometrical shapes (*shapes* task), was used as high-level baseline for the comparison between the brain activations associated with the experimental conditions.

4.1. Method and Procedure

Participants

Thirteen right-handed volunteers (8 female, mean age=25; SD=4.57) participated in the fMRI experiment. All of them had normal or corrected-to-normal vision and gave their written consent to take part in the study.

Ethics Statement

The experiment was approved by the Ethic Commission of the Medicine Faculty of RWTH Aachen.

Stimuli

Participants were asked to perform two separated tasks. In the experimental *objects* task, stimuli were grey-scaled pictures of 10 graspable objects. According to the task demand (i.e. to decide whether an object can be used to eat or drink or not), 5 of them could be used to eat or drink (mug, fork, wineglass, pot, spoon) and 5 could not be used for this purpose (key, toothbrush, comb, screwdriver, watering can; Figure 12). For each object, we presented the usual (i.e. traditional) version and a structurally modified (unusual) version. The ratio behind the choice of the unusual stimuli was the same of the Studies 1 and 2 (i.e. the objects were formed by a functional and a graspable part, and, although structurally modified, they still remained fully recognizable). In the high-level baseline task, stimuli were grey-scaled pictures of two geometrical shapes (triangle and square), centrally presented on the monitor.

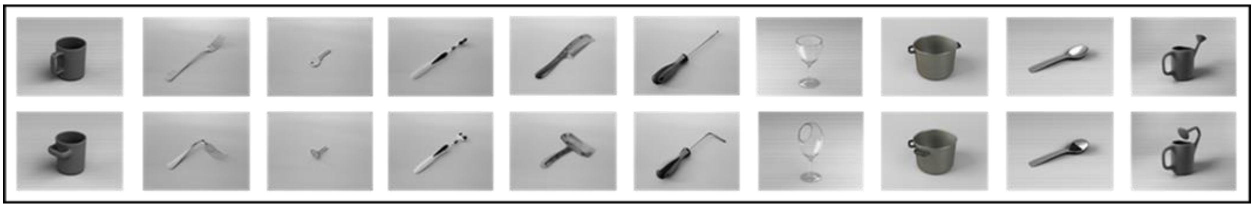


Figure 12. Stimuli: Usual objects (above) and their corresponding Unusual versions (below).

Apparatus

The experiment was conducted on a 3T scanner (SIEMENS MAGNETOM Prisma), using standard gradients and a 20-channel head coil. Participants laid their back on the scanner bed while having a foam pillow placed under their legs/knees. An MRI compatible ergonomic keypad was placed over their abdomen in a comfortable position for them to press the response buttons with their left thumb and index finger. Their right arm laid comfortably on the bed, parallel to their trunk.

Stimuli presentation was controlled by the *Presentation* software (Neurobehavioral Systems, http://www.neurobs.com). Presentation triggered fMRI measurement via serial port interface between the PC and the scanner and projected the stimuli on an MR-compatible monitor placed behind the scanner. Because of a small mirror integrated within the head coil, participants could see the monitor behind them**.**

Procedure

Participants were tested in 5 experimental sessions in 5 different days. Before starting each session, participants were asked to fill in the MRI compatibility questionnaire, to ensure they could undergo the fMRI session.

During each session two different tasks were performed. Before entering the scan, participants read paper printed instructions, which were also displayed again in a shorter version on the monitor behind the scanner before the beginning of each task.

In the *shapes* task participants had to discriminate between two geometrical shapes (square and triangle), by pressing one of two buttons on a keypad with their left thumb or index finger and trying to be as fast and accurate as possible. This task included 50 trials, in which 25 triangles and 25 squares were presented. The order of stimulus presentation was randomized across sessions but was the same for all the participants (pseudorandomized presentation) and the association between the stimuli and the correct response was counterbalanced between subjects.

After this, the *objects* task was performed, where participants had to judge whether the object displayed could be used to feed oneself (eat or drink) or not. This task included 200 trials. Usual and unusual objects were separately presented grouped in miniblocks of 5 objects, in which objects used or not used feeding oneself were mixed presented. Therefore, 20 miniblocks of 5 usual objects and 20 miniblocks of 5 unusual objects were randomly presented, resulting in a total amount of 200 trials. Participants had to response on the same keypad as in the *shapes* task, by pressing one of two buttons with their left thumb and index finger as quickly and accurately as they could. Literature showed that the orientation of the graspable part of an object can affect the motoric response of the spatially corresponding hand performing the action (e.g. Tucker and Ellis, 1998). Therefore, in order to avoid any motor bias due to correspondence between the responding hand and the orientation of objects' handle, participants responded always with their left hand and objects were always presented with their handle orienting to the left. We decided to do so, because of the intention to collect data also from apraxic patients, who will be asked to use their left hand, as their left hemisphere lesion could affect the use of their right hand (e.g. Goldenberg, 2009). The presentation order of the miniblocks was identically randomized across sessions for all the participants (pseudorandomized presentation) and, as in the *shapes* task, the association between the stimulus and the correct response was counterbalanced between subjects. This task was split into two parts, with 100 trials each. Between one half and the other, structural anatomical images were collected. This phase lasted about 5 minutes, during which participants did not have to do any task and an entertaining short video was shown to them.

In both the *shapes* and the *objects* tasks, the time line of the trials was the same. Each trial started with a fixation cross lasting 1000 ms, after that the stimulus appeared on the screen and remained visible for three seconds, during which participants had to respond. After the three seconds, in the case of a wrong response the feedback “wrong” was displayed, whereas in the case of a missing response the feedback “missing” was displayed. Instead, when participants press the button too early (i.e. before the stimulus onset), they received the “too early” feedback. These feedbacks were displayed for one second on the screen. No feedback was presented in case of correct response and a blank screen was displayed for one second. After the feedback, an interstimulus interval blank screen lasted for 7 seconds (Figure 13). This allowed the brain activation associated with the stimulus processing to go back to a basic level.

In addition to these two main tasks, participants were asked also to perform an “oddball task”. We decided to add this part to keep a high level of attention and to avoid participants getting too tired. Oddball task included a total of 14 trials, which were pseudorandomly presented mixed with the trials of the two main tasks. Four trials were presented during the *shapes* task and 10 during the experimental task. They were excluded from the analysis, as we were not interested in data from this performance. For each trial, at the onset of three dices on the screen, participants had to decide whether the sum of the dots resulted in an odd or in an even number and responded by pressing on the two buttons with their left thumb or index finger. In this case, the association between the stimuli and the correct responses was kept the same.

The total duration of each session was approximately one hour and half (30 minutes for the preparation phase before going into the scanner and 60 minutes for the measurement phase inside the scanner).

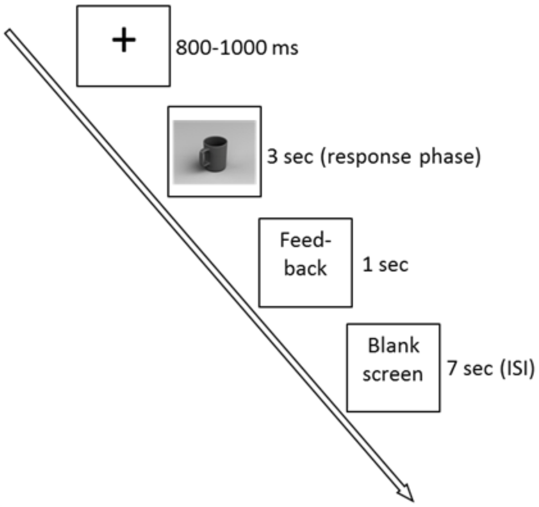


Figure 13. Schematic representation of the timeline of a single trial.

4.2. Behavioural data analysis

We were interested in reaction times (RTs) from *objects* task only and we analysed the time of correct trials only. Therefore, we discarded errors (1,57%), omissions (3,01%) and "too early" responses (0,1%). RTs faster than 200 ms and slower than 1300 ms were excluded (5,18% of the total correct trials). A repeated-measures ANOVA was carried out considering two within-subjects factors: Type of objects (Usual vs Unusual); Function (objects used to feed themselves or not; i.e. Feed vs NoFeed objects).

4.3. fMRI data acquisition and preliminary analysis[3]

fMRI data acquisition

Imaging was performed on a 3 Tesla scanner (SIEMENS MAGNETOM Prisma) using a 20 channels head coil. For each participant, during each session 1624 functional scans were acquired (332 of the *shapes* task and 1292 for the *objects* task) in 32 axial slices of 3 mm thickness with interleaved slice acquisition using an EPI sequence, a repetition time (TR) of 2000 ms, echotime (TE) of 28 ms, a flip angle (FA) of 77°. The in-plane resolution was 3 × 3 mm. T1-weighted anatomical images were also acquired for all participants, with a 3D MPRAGE sequence (192 slices, TR 1900 ms, TE 2.21 ms, FA 9°, resolution 1 × 1 × 1 mm).

fMRI data preliminary analysis

Data analysis was performed with SPM12 (Statistical Parametric Mapping Software; The Welcome Trust Center for Neuroimaging, University College London, London, UK) running on MATLAB (The Mathworks, Inc., Natick, MA) and with the SPM Anatomy Toolbox (Eickhoff, Stephan, Mohlberg, Grefkes, Fink, Amunts and Zilles, 2005).

Despite the data are still preliminary, they refer to 5 sessions of 6 subjects, whose data analysis could be completely carried out (i.e. all the five sessions were analysed, providing a total amount of 30 datasets). As further complex motion corrections are needed for the data analysis of the other subjects, it will require additional time to process the data. The procedure used to analyse the data of the subject was the following.

The slice-timing of the datasets of each session was first corrected. For spatial motion corrections, a mean image was created by realigning all the images to the first image and

[3] This research was supported by the Brain Imaging Facility, a facility of the Interdisciplinary Center for Clinical Research (IZKF) Aachen within the Faculty of Medicine at RWTH Aachen University.

subsequently all the images were realigned to the mean image. T1 image was then co-registered to the mean image of the realigned functional images.

The functional and structural images were normalized to the MNI template (Montreal Neurological Institute; http://www.mni.mcgill.ca/). Normalization parameters were applied to all EPI images and the T1 image. The images were resampled to 2mm × 2mm × 2 mm voxel size and spatially smoothed with an 8 mm full width half maximum isotropic Gaussian kernel. The quality assessment of the data was then improved by the calculation of the percent-signal-change (PSC), using the AQUA script (Stöcker, Schneider, Klein, Habel, Kellermann, Zilles and Shah, 2005). A two-level approach was subsequently used to analyse the data, using a General Linear Model (GLM). The single-subject level analysis was carried out over all the 30 experimental sessions and modelled considering the factor Type of objects (i.e. Usual vs Unusual objects) as implicit baseline and the 6 motion parameters obtained in the realignment step and the PSC values as covariates of no interest (7 covariates in total). "High level" baseline contrasts were performed contrasting the activations observed in the *objects* task (i.e. the experimental task) against those observed in the *shapes* task (i.e. the control task). In this way, the activations related to the pure processing of usual vs unusual objects were obtained and those to visual shape elaboration exluded. Then, the group-level analysis was performed by pooling the data referring to each object category across all the sessions analysed. Significant statistical threshold was set at $p < 0.05$ (false discovery rate correction, FDR).

4.4. Behavioural results

Significant main effects did not emerged for neither the Type ($F_{(1,12)}$= 619, p= .447) nor the Function ($F_{(1,12)}$= 121, p= .734) factors. A significant Type x Function interaction emerged ($F_{(1,12)}$=21, p=.001; Fig. 10B). RTs for Usual Feed objects (mean=721 ms; SD=82.09) were faster than for Unusual Feed objects (mean=739 ms; SD=81.17; $t_{(12)}$ = -4.9; p<.001). Moreover, RTs for

Usual NoFeed objects (mean=733 ms; SD=68.98) were slower than for Unusual NoFeed objects (mean=719 ms; SD=70.38; $t_{(12)} = 2.8$; p=.016; Figure 14). The other comparisons were not significant (all Ps>.05).

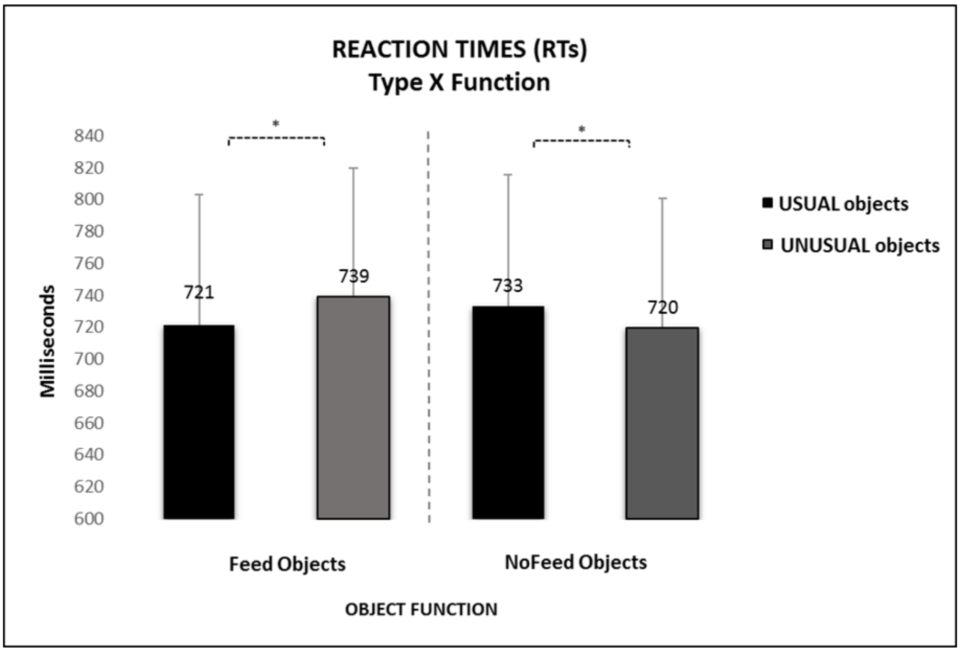


Figure 14. Mean reaction times (RTs). Error bars indicate standard deviation. Statistically significant comparisons are shown.

4.5. fMRI data results

As the patterns of activations elicited by the usual and the unusual objects were, as expected, very similar, no relevant difference between them was revealed by the contrast analysis. Therefore, we focused on the main activations referred to the usual and unusual objects separately, which highlighted a differential recruitment of areas belonging to the ventral, ventro-dorsal and dorso-dorsal streams.

Main activations for the Usual objects

The analysis of the processing of Usual objects revealed clusters of activation (Table 2) which included occipito-temporal areas areas (left and right Lingual Gyrus, left Cuneus), the right

Superior Parietal Lobule (SPL) and the right Inferior Parietal Lobule, IPL (i.e. the anterior Supramarginal Gyrus, aSMG; Figure 15).

Table 2. Peak voxel coordinates in MNI space of significant activation clusters for Usual objects

MNI Coordinates			Anatomical Location
x	*y*	*Z*	
64	-20	24	Right anterior SupraMarginal Gyrus (aSMG)
58	-36	48	Right Superior Parietal Lobule (SPL)
-12	-82	30	Left Cuneus
10	-82	-12	Right Lingual Gyrus
-8	-72	-10	Left Lingual Gyrus

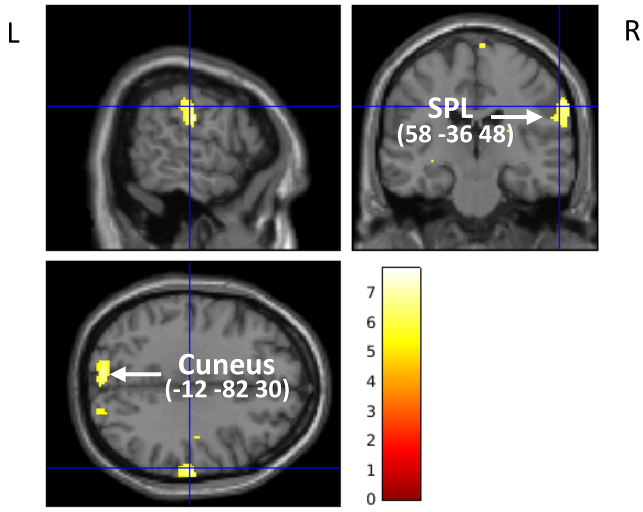


Figure 15. Pattern of activations observed for the Usual objects. The statistical images show results at a threshold of $p < .05$ (FDR corrected). Coordinates are in Montreal Neurological Institute space. Abbreviations: SPL = Superior Parietal Lobule.

Main activations for the Unusual objects

The main activations for the processing of the Unusual objects, although partially similar to those observed for the Usual ones (Table 3), were stronger and more bilaterally located. Bilateral cluster of activations were found in the occipito-temporal areas (Lingual Gyrus and Cuneus), in the SPL and in the IPL (i.e. aSMG). Moreover, a cluster of activation was found in the let precuneus (Figure 16).

Table 3. Peak voxel coordinates in MNI space of significant activation clusters for Unusual objects

MNI Coordinates			Anatomical Location
x	y	Z	
64	-18	24	Right anterior SupraMarginal Gyrus (aSMG)
-60	-32	38	Left anterior SupraMarginal Gyrus (aSMG)
48	-44	62	Right Superior Parietal Lobule (SPL)
-46	-50	38	Left Superior Parietal Lobule (SPL)
-4	-58	72	Left Precuneus
-10	-82	30	Left Cuneus
10	-76	-10	Right Lingual Gyrus
-8	-72	-10	Left Lingual Gyrus

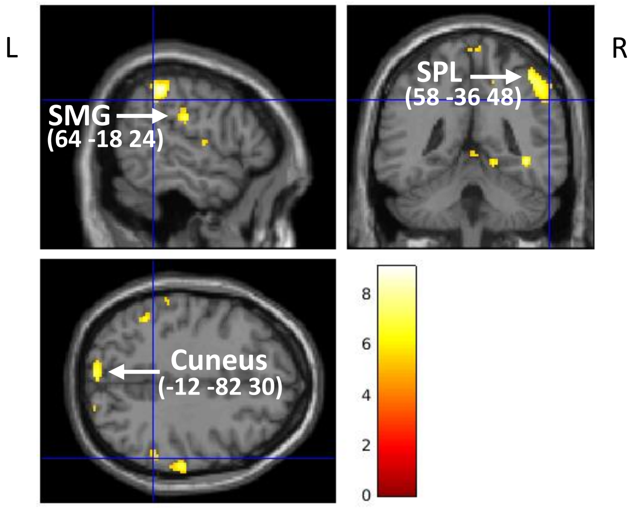


Figure 16. Pattern of activations observed for the Unusual objects. The statistical images show results at a threshold of $p < .05$ (FDR corrected). Coordinates are in Montreal Neurological Institute space. Abbreviations: SPL = Superior Parietal Lobule; SMG = Supramarginal Gyrus.

4.6. Discussion

This fMRI investigation was driven by the recent evidence supporting the different involvement of the ventro-dorsal and dorso-dorsal stream in the processing of stable and variable affordances, respectively (Sakreida et al., 2016). Indeed the former ones are supposed to be related to the processing of the functional manipulation-related properties, while the latter ones refer to temporary object properties, related to the structural object features (Buxbaum, 2017; Binkofski and Buxabum, 2013; Kourtis et al., 2018; Binkofski and Buccino, 2018) As regards the present work, the aim was to investigate the processing of the *unusual* objects and the neural involvement associated with the elaboration of their structural alteration, while their function-related identity was recognizable and accessed (by the mean of the experimental task).

Despite the results are still preliminary, the specificity of this experimental procedure (i.e. the high number of sessions per participant) allows to consider the data stable.

First, the data showed a wide overlap between the patterns of activation. Indeed, as hypothesised the usual and unusual objects elicited very similar patterns of activations, and this was induced by the semantic nature of the task (deep semantic processing), indicating the involvement of common activities between the processing of the two categories of objects. This is evidenced by the recruitment of the ventral (e.g. occipito-parietal areas), the ventro-dorsal (i.e. IPL, and aSMG in particular) and the dorso-dorso (i.e. SPL) streams. This result highlights that the unusual objects are semantically and functionally recognized as their usual counterparts (i.e. the usual objects) and support the (experimental) assumption that they are not elaborated as meaningless objects. Rather, they are meaningful objects whose categorization is made more difficult because of the violation of their structure, which induces to a major recruitment of the processing resources, while their recognition is driven by their clear semantic and functional meaning. This augmented difficulty in the categorization is supposed also to be revealed by the stronger activations in the case of the unusual objects in both the dorsal streams. Crucially, the unusual objects activated bilaterally both the ventro-dorsal stream (i.e. the IPL and the Precuneus) and the dorso-dorsal stream (i.e. the SPL).

As regards the dorso-dorsal stream, the results are in line with our expectations. The hypothesis was that unusual objects should induce a greater processing load, because a stable affordance (i.e. the shape) needs to be re-coded and requires to be treated as a variable one. Results show that the structural variation of the unusual objects induced to a greater involvement of the on-line visual processing and control. Therefore, they are in line with previous literature (see Binkofski and Buxbaum, 2013; Binkofski and Buccino 2018) and with the findings of Sakreida and colleagues (2016) about the processing of the variable affordances relying more on the dorso-dorsal processing.

As regards the ventro-dorsal stream, albeit the greater activation of IPL for unusual objects could be surprising compared with the findings of Sakreida and colleagues (2016), it is not if the nature of the task demand is considered. Indeed, in the metanalysis (Sakreida et al., 2016) the major distinctions between variable and stable affordance were established according to the presence or the absence of a change in the planned action *during* the task performance, due to the variation of one or more object characteristics. However, in the present study the task demand, i.e. categorizing according to a specific function-related property (i.e. whether the presented object was used to eat/drink or not), led participants to treat unusual objects as their usual counterpart, considering, as said above, the stimuli as two versions of the same object with the same function. Therefore, the increased difficulty in attributing the function to the unusual objects explains the greater IPL activation for this category of objects. Indeed, a *crucial point* is that unusual objects are neither meaningless nor “functionally unfamiliar”, being the “usual function” clearly attributed to them. The greater activation in the inferior part of the parietal lobule reflects the mechanism of attributing a known function to a “visually unfamiliar” object. In line with this result, Kourtis and colleagues (2018) showed the neural activations corresponding to the “function congruency effect” (i.e. a facilitation of the motor responses spatially corresponding to the location of the part of the object that indicated its function). The comparison of the neural activation of functionally congruent vs incongruent trials showed a stronger activation in two clusters, one in the SPL and a larger one in the IPL. Crucially, the functional processing of the objects was not required, since the participants had to respond according to the direction of an arrow displayed over the object pictures. These results indicated that functionally congruent trials automatically evoked a stronger activation of the action selection, and of both on-line control mechanisms (in charge of the dorso-dorsal stream processing) and the motor planning of object-directed actions (in charge of the ventro-dorsal stream processing). In the present study, these mechanisms were enhanced by the task demand and became more evident with unusual objects that needed more resources being "more difficult" meaningful objects. There is some evidence that when unknown objects are associated with a specific way to be manipulated (e.g. Weisberg et al., 2006), or the pattern of unknown gestures become familiar (e.g. after several repetitions; Grèzes, Costes and Decety, 1999), areas in the ventro-dorsal streams are more recruited.

An alternative interpretation is that the "technical reasoning" (see Osiurak and Badets, 2016 for a detailed review) is responsible for the enhanced activity in the IPL. According to this *reason-based theory*, reasoning about object physical properties drives the ability to use the objects according to a non-declarative knowledge about physical principles, rather than stored sensorimotor representations (i.e. manipulation knowledge; Buxbaum and Kalénine, 2010). The neural substrate of the reason-based mechanism is in the left IPL. According to the reason-based theory, unusual objects would induce to a greater processing due to the need of reasoning about the possible way to use them. The unusual objects here used represent a compromise between the requirements of using single tools (more related to the manipulation knowledge) and of using novel tools or the unconventional use of familiar tools (involving the tool and the related object, and more related to the mechanical reasoning). Therefore, they represent good candidates to investigate whether the manipulation knowledge and the technical reasoning can coexist and be, for example, hierarchically organised.

At last, on the behavioural side, different patterns of RTs according to both the type of objects (Usual vs Unusual) and their function (Feed vs NoFeed) was found. For objects used to eat/drink, the usual objects were advantaged, whereas, in the case of objects that cannot be used to eat/drink, a facilitation for unusual objects emerged. This modulation according to the function could be due to the task demand, leading to a different processing mechanism and dorsal streams' involvement. When the object function matches the target function (required by the task demand), usual objects find full correspondence to the object semantic and functional representations activated by the ventral and the ventro-dorsal stream for the response decision. This is not the case for unusual objects, whose motor simulation has to be recoded according to their modified structure, and therefore response decision requires more time. On the other hand, when object function does not match the target function, unusual objects can take advantage from their incongruence with experience-based sensorimotor representations activated by the task demand. In this case, a visually guided analysis gives its contribution to the response decision, leading to faster RTs.

Thus, taken together, the results revealed that the unusual objects represent a class of stimuli that is able to employ the resources needed for the object processing at a different extent, being their semantical and functional meaning equal.

4.7. Further directions

Besides the classical statistical inference approach (i.e. linear general model), data will be analysed also using a data-driven approach (i.e. the Multivariate Pattern Analysis -MVPA-), which is based on learning-based inferences (Bzdock, 2017). This kind of analysis needs a big amount of data to work on, and this is the reason why we decided to collect data from 5 sessions for each participant and why we adopted this kind of blocked presentation. In brief, in the learning-based statistics a two-step procedure is applied. In the first one, one part of the data (training data) is used to create an algorithm able to predict activation patterns and to extrapolate them from other samples (i.e. different individuals). In the second step, this algorithm is tested on a smaller amount of independent data (test data). The advantage of using such a kind of analysis is that it better represents what data “say”, making least assumptions as possible and using an exploratory (more than confirmatory) approach (for a review see Bzdock, 2017). This kind of analysis will allow us to highlight the differences in the patterns of common activities between the processing of usual and unusual objects, specifying the contributions of the tool-devoted networks (for the use of the same analysis procedure, see Horoufchin, Bzdock, Buccino, Borghi and Binkofski, 2018).

Chapter 5

General discussion

The aim of this research was to investigate the contribution of the two cognitive/neural systems involved in object processing during different phases of object-directed actions, when it is supposed that objects' properties that are relevant for actions (i.e. the affordances) are differently weighted, according to the request of the task.

In Chapter 1 the principal models were explained, defining a recent concept of affordances (i.e. stable vs variable affordances; Borghi and Riggio, 2009; 2015) and the cognitive systems thought to be in charge of their processing (i.e. the Function vs Structure systems, respectively; Buxbaum and Kalénine, 2010; Buxbaum, 2017. At a cognitive level, while the Function system is supposed to process invariant function-related information mainly based on stable affordances, the Structure system is thought to process the temporary visually-derived information, constituting the variable affordances. Moreover, anatomically speaking, the Function system relies on the ventro-dorsal stream and the Structure system on the dorso-dorsal stream, (Rizzolatti and Matelli, 2003; Binkofski and Buxbaum, 2013).

The novelty of the research was based on the type of stimuli here introduced and compared: usual and unusual objects. While usual objects consisted of a very familiar version of daily used tools, the unusual objects were a modified version of usual ones in that their structure was modified but they still remained clearly recognizable in terms of both their identity and function. Because of the structural modification, however, the planning of use-related gestures had to be adapted. Indeed, as the stored sensorimotor representations related to the use of the objects refer to their (invariant) shape (i.e. a stable affordance), they fit for the processing of usual objects. Conversely, in the case of unusual objects, object structure is represented as a “temporary” characteristic (i.e. a variable affordance), thus requiring the contribution of the visually-driven analysis to a greater extent. This is the crucial characteristic of these stimuli, which are unfamiliar (but not meaningless) in terms of their structure and remain familiar because of their recognizable function. Indeed, previously employed unfamiliar objects were novel or uncommon objects (e.g. Vingheroets 2008; Dawson et al., 2010; Bellebaum et al., 2013; Weisberg et al., 2007), whose manipulation knowledge was not highly consolidated. Thus, the systems processing stable and variable affordances here were differently recruited by the altered structure of unusual objects, requiring a greater involvement of the visually-guided analysis (i.e. the Structure system), while the goal of the action could remain the same for both the object categories.

Thus, the unusual objects constitute a particular class of stimuli allowing to modulate the contribution of the systems devoted to the processing of the object properties. In all the reported studies the task demand required to process a function-related property of the objects to ensure a deep processing, leading to access the knowledge about the way they are manipulated on the base of previous experiences (i.e. with usual objects). A first behavioural study (Chapter 2) investigated the complementary computation of stable (use-related) and variable (structure-related) affordances, during different action phases (i.e. planning vs. execution). Participants were required to perform a semantic categorization task on both usual and unusual object pictures presented in separated blocks. They had to press one of two lateralized response keys (Experiment 1), or to perform a reach-to-grasp movement, which was supposed to induce a motor simulation (Experiment 2).

Two main results emerged. First, unusual objects were recognized and processed in the same way of their usual counterparts, with the functional part (i.e. the object part associated with the performance of the function they are created for) being focused (Experiment 1). Second, the contribution of the Function and the Structure systems differently emerged in planning and executing a movement, depending on the variation of object structure (i.e. a stable affordance usually used to convey functional information about the objects). A major involvement of the Function system seemed to emerge during the planning phase with usual objects, driven by the ventro-dorsal stream, and a major involvement of the Structure system emerged during the programming phase on unusual objects, relying on the dorso-dorsal stream processing. Interestingly, the order in which the two object categories were presented, especially when an actual movement is required, made the different involvement of the two systems come to light, demonstrating their ability to modulate the recruitments of the cognitive/neural systems (Experiment 2).

Chapter 3 focused on a kinematic investigation of the object-directed, grasp-to-use gestures in condition of prevented vision, toward either usual and unusual objects. The occlusion of vision and the use of a temporal delay in the execution of the use-related actions were expected to modulate the weight of the stable and variable object features, according to the different timing of the Function and the Structure systems. Indeed, on one hand the processing of functional properties (Jax and Buxbaum, 2010; Valyear et al., 2011) in charge of the Function system, elicited here by the task demand, is driven by a relatively long-lasting activation of the ventro-dorsal stream (Binkofski and Buxbaum, 2013). On the other hand, visually-derived properties in charge of the Structure system, processed on-line in the dorso-dorsal stream (Binkofski and Buxbaum, 2013; Borghi e Riggio, 2015), are supposed to rapidly decay when the vision is prevented (Goodale, et al., 2005; Westwood and Goodale, 2003). Therefore, by progressively decreasing the availability of the visual information, the involvement of the Structure system was modulated, and the employment of the unusual objects allowed to observe this modulation. Participants were required to grasp the (usual and unusual) objects and to effectively demonstrate how to use them in three experimental conditions. Condition 1 represented the baseline (i.e. immediate grasping in condition of full vision). Condition 2 represented a middle-way condition (i.e. immediate grasping with no vision), in which a conflict between the two dorsal streams was generated because of the decaying of visual information during the movement execution. At last, condition 3, requiring a 3-second delayed grasping with no vision, implied that stored experience-based sensorimotor representations about object manipulation prevailed in guiding the action.

Crucially, this study was designed to investigate three distinct phases of the grasp-to-use action performance: the planning phase, the reaching phase and the actual use phase. They demonstrated to be affected by the type of object in relation to the conditions of visual prevention, that is immediate (Condition 2) vs delayed (Condition 3) grasping with no vision. In the planning phase, the main kinematic landmark of grasping (i.e. the MGA) showed that, generally (i.e. with usual objects), the contribution of the Structure system (i.e. the processing of the object structure) became less and less prominent with the progressively higher prevention of vision. Conversely, unusual objects required more resources from the visually-guided analysis, as MGA was based on the exact metrics of the object even in absence of vision. The decay of spatial information in the reaching phase (causing progressively longer MTs and more spatial explorations) reflected the effect of the prevention of vision on the performance, and results supported the hypothesis that unusual objects rely more on the dorso-dorsal stream processing (representing the neural base for the Structure system) than the usual objects: *Structural* visually-derived information about unusual objects required more resources, to the detriment of the *spatial* information, depending on the same neural substrate. This therefore led to a greater number of explorations for the unusual objects. Finally, the errors committed toward unusual objects in the actual use phase showed the outcomes resulting from a “functionally-predominant” vs a “structurally-predominant” analysis, which compete in condition of time constraints and visual decay. As in this study objects were randomly presented, future investigations may clarify other factors influencing processing selection/modulation, as, for example, the effect of the previous trial (using fixed and separated presentation of usual and unusual objects) or the effect of learning on kinematics with unusual objects (using multiple repetitions of the same unusual objects within the same experimental condition).

To summarize, results reported here support the different involvement of the two cognitive/neural systems, adding evidence related to: i) the phase of the action, with the Function system involved in the planning phase and the Structure system in the execution phase; ii) the object familiarity, with the Function system involved in the processing of usual (familiar) objects and the Structure system involved in the processing of less familiar (i.e. the unusual) objects (literature so far referred only to unfamiliar and novel objects; see Buxbaum and Kalénine, 2010; Buxbaum, 2017).

At last, a fMRI investigation of the neural basis underlying the processing of the two categories of objects was carried out (Chapter 4). This study was conducted on the base of a previous meta-analysis on the brain activations triggered by the processing of stable and variable affordances (Sakreida et al., 2016), indicating that they rely on the dorso-dorsal and ventro-dorsal activity, respectively. Participants were required to categorize usual and unusual objects according to a functional characteristic, similarly to the first behavioral study presented in Chapter 2. Indeed, the access to the function of the objects was supposed to highlight the effect of the structural variation of the unusual objects in processing use-related actions and to confirm that it required a greater contribution of the visual control by the dorso-dorsal stream.

Results showed that the processing of unusual objects recruited both the dorso-dorsal and the ventro-dorsal stream to a greater extent in comparison to usual objects. This pattern of activation, on one hand, confirmed the major role of the visuomotor control (by the dorso-dorsal stream) with the unusual objects, on the other hand, it highlighted that they also required a stronger ventro-dorsal activation to be assigned with their “usual function”. However, results are still preliminary and still do not specify the activation/inhibition pattern of activity of the two dorsal streams while processing object properties (i.e. what the patterns of activation exactly reveal about their cooperation).

In conclusion, the processing of unusual objects has revealed that this category of objects could be helpful in clarify the neural bases of our ability to use objects ant the role played by the object characteristics, given the intention to interact with them in a purposefully way. Indeed, unusual objects could be considered a relevant class of stimuli for at least two reasons. First, they could fill a gap in the categories of objects previously used in research, representing a middle-way class between familiar and unfamiliar/novel objects. They could be considered as an additional tile, in the way objects can be classified according their familiarity (i.e. familiar, unusual, unfamiliar/novel, meaningless objects). Second, they could be useful in representing a more ecological class of stimuli. Indeed, they resemble the situation in which the interaction with objects occurs without the optimal perception of the object, like, for example, the contexts where a familiar object is perceived in a non-canonical perspective (which are also employed in neuropsychological investigations about the ability to recognize objects; Warrington and Taylor, 1973).

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