

Enactivism, Representations and Canonical Neurons

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Abstract

Enactivists often claim that since perception is one with action, it does not involve representations, hence perception is *direct*. Here we argue that empirical evidence on neural activity in the *ventral premotor cortex* confirms the enactivist intuitions about the unity of action and perception. But this very unity requires the detection of the action possibilities offered by the objects in the environment, which in turn involves certain representational processes at the neural level. Hence, the enactivist claim that perception is direct is wrong, or at least ambiguous and potentially misleading: in one important sense perception involves representations.

Keywords: Enactivism, Visuomotor Representations, Canonical Neurons, Affordances, Transparency of Perception, Sensorimotor Processes, Ventral Premotor Cortex, Direct Perception

Introduction

In current cognitive studies various different approaches are called enactivist, as they stress that our cognition is based on the unity of action and perception (henceforth: UAP): this is how we perceive and act upon the sensorimotor contingencies (i.e. affordances) found in the environment. On the basis of UAP enactivism claims that representations are not involved in perception, and perception is direct. There is wide empirical evidence in neuroscience confirming and explaining UAP and the role of affordances, but these explanations and confirmations crucially involve subpersonal representations: so we argue, against enactivism, that perception is indirect.

In § 1 we report the basic enactivist intuitions—exemplified by Noë 2004—on UAP, affordances, and the related claim that perception is direct. After focusing especially on the relation between enactivism and the concept of representation, we then turn to the two basic goals of this paper:

- A) In § 2 we show that empirical evidence on neural activity in the *ventral pre-motor cortex* confirms the enactivist intuitions about UAP and affordances. However, we also make clear that we can map the external objects thanks to the fact that the neural correlates of UAP perform representational processes.
- B) Therefore in § 3 we claim that the enactivist doctrine of direct perception is potentially ambiguous, and might be wrong in an important sense: since UAP involves representations, perception is indirect.

This is not a survey of the various kinds of enactivism, each with its own philosophy concerning UAP, nor do we discuss the most recent debates on them¹. For despite their differences, these various views share the intuition of UAP, and we stress that this intuition is empirically well confirmed. It is remarkable that the literature on enactivism never mentions these empirical findings, and above all, it does not notice the lurking contradiction between UAP and the claim that perception is direct.

1. Enactivism and UAP

According to Gibson (1986) we can explore reality through an indivisible movement-perception system, perfectly *attuned* with the visual invariants in the *umwelt*, that allows us to act: perception controls movements and movements are fundamental to get perceptual information. Gibson's primary concept is that of *affordance*²: the environmental opportunities for action that an object offers to an agent. In his view we can profit of affordances thanks to UAP: realizing what an object is (in the visual dimension) is realizing what we can do to and by it (in the motor dimension)³. Thus, against a common idea of classical cognitive sciences, he claims that, since our perceptual system *resonates* to the properties of objects, perception is direct.

Enactivism (also called *sensorimotor paradigm*) is heir to his view: it “question(s) the centrality of the notion that cognition is fundamentally representation” (Varela, Thompson and Rosch 1991: 9), and it was mainly developed in Clark 1998, O'Regan and Noë 2001, 2004. Many cognitive approaches sail under this banner, but they share at least these assumptions:

- E1 UAP: i.e., perception consists in (and depends on) mastery of sensorimotor skills: it is based on the interdependent availability of perceptually conducted motor behaviour associated with the related sensory consequences, and it allows us to act upon the objects in accordance with their *sensorimo-*

¹ See Hutto and Myin 2013; Thompson 2007; Stewart, Gapenne and Di Paolo 2010; Gangopadhyay and Kiverstein 2009.

² Affordances are a visual process making us aware of the possibilities of action upon the object, not to be confused with the motor act we can perform on the (object itself on the basis of the) affordance. Which affordances we get in a given situation depends both on the characteristics of the environment (optic array, outlines, objects), and on the acting individual (its body, skills, etc.). Obviously, the relationship between motor acts and affordances can change with respect to different purposes.

³ See § 2.

tor contingencies⁴, i.e., affordances, the various ways objects afford our behaviour.

E2 It follows from E1 that we have an immediate visualization of the sensorimotor contingencies and that perception is direct.

These basic assumptions are exemplified in Noë's account of enactivism, one of the most influential: perception "depends on the possession and exercise of a certain kind of practical knowledge (*know-how*)" (Noë 2004: 33). What we perceive is in function of the way we act, and the way we act is an aspect of perceptual processes. Perception (in particular visual perception) has been evolved to help motor control, it is part of a procedure aimed at achieving some purpose (Noë 2009). The experience of an object consists in the set of actions involved in perceiving the object (O'Regan 2011; Zipoli Caiani 2013b; for a complete review see Hutto and Myin 2013, Ferretti, forthcoming-b).

[...] perceiving is a way of acting. Perception is not something that happens to us, or in us. It is something we do. [...] The world makes itself available to the perceiver through physical movement and interaction [...] all perception is touch-like in this way: perceptual experience acquires content thanks to our possession of bodily skills. What we perceive is determined by what we do (or what we know how to do) (Noë 2004: 1).

Like Gibson, Noë (2004: 2) rejects the view of perception inspired by Marr (1982), whereby perceptual processes in the brain create detailed inner representations of the external environment. Instead, he claims that perception is direct. He rejects the "snapshot conception"⁵, according to which the world is given to us as rich in details all at once: he denies that when we see we *represent* the whole scene in consciousness all at once in the way a photograph does (Noë 2004: 63, 72-73, 218-219). "There's no need to build up a detailed internal model of the world" (Noë 2004: 50). Our attention permits us to perceive just a portion of the scene and only a few objects. This is possible thanks to "the way in which objects structure and control our movements and our sensory stimulation" (*ibi*).

According to some authors enactivism nonetheless admits a form of representations, closely tied to bodily activities (or skills) (Wilson 2004: 186; Menary 2006: 3-5). In fact, at least in one passage Noë grants that "No doubt perception depends on what takes place in the brain, and very likely there are internal representations in the brain (Noë 2004: 2). But it is not clear what these representations are. We agree that there are representations, but in § 2, while supporting E1,⁶ we offer a clearer analysis of what they are, and how they can explain bodily skills. In our opinion, the fact that we do not *represent* the entire scene does not mean that the objects we "select" on the scene are not represented; in fact, the perception of sensorimotor contingencies requires subpersonal visuomotor

⁴ Noë treats 'sensorimotor contingencies' as a near synonymous of 'affordances': see Noë 2004: 105-106.

⁵ See Noë 2002. He also uses experiments like those concerning *inattentional blindness*, *reverse lenses (inverting goggles)* and *change blindness*.

⁶ Of course not all perception is aimed to action. But here we will focus on the precise portion of perception that is functional to action (see Milner and Goodale 2005; Jacob and Jeannerod 2003).

representations (henceforth: SV representations). Here we do not focus on the snapshot conception of representation. We just claim that rejecting the “snapshot conception” is not sufficient to show that perception is direct, i.e., that no representations are involved in perception. Therefore in § 3 we reject E2.

2. Empirical evidences

Studies on monkeys show that the brain’s motor system is not involved only in executive functions. The motor system includes area 6, the premotor cortex, occupying the posterior portion of frontal lobe (the cortical region directly involved in voluntary movement), and area 4, the primary motor area (Fig. 1). Area 6 is not homogeneous, and it can be divided into dorsal premotor cortex (F7 and F2) and ventral premotor cortex (F4 and F5) (Fig. 2).

We will particularly focus on F5, which is directly connected with the primary motor area (area 4): it receives nervous signals from the parietal lobe, which for a long time was considered an associative area for sensory operations. Other studies demonstrated that the motor cortex influences the perceptual side of the parietal lobe, which is now considered a part of the motor brain (Mountcastle *et al.* 1975; Sakata *et al.* 1995).⁷ Thus, the idea of a *motor system* exclusively involved in motor roles is now dismissed: the motor cortex is basic for sensory operations as well. As we shall see in § 2.2, these evidences already confirm UAP;⁸ but more can be found by studying F5 (Matelli, Luppino, Rizzolatti *et al.* 1985).⁹

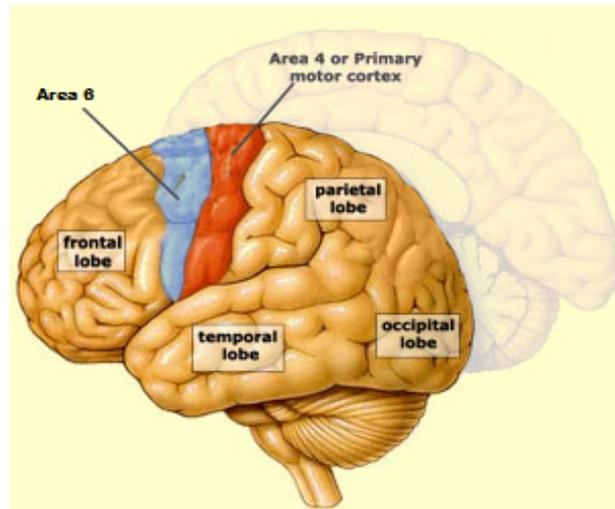


Fig. 1. Cortical division into lobes.¹⁰

⁷ Cited in Gallese 2000: 27; see also Rizzolatti and Sinigaglia 2006.

⁸ More evidences in § 2.2.

⁹ Cited in Gallese 2003: 1235. Here we do not discuss the problem of the two cortical visual streams in relation with these points: see Noë and Thompson 2002; Rizzolatti and Sinigaglia 2006; Fridland 2012.

¹⁰ Adapted from: <http://www.docstoc.com/docs/122202947/9-Corteccia-motoria>

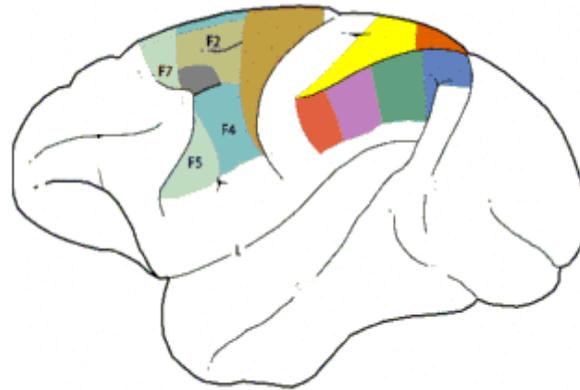


Fig. 2. Premotor cortex (area 6): Dorsal (F7 and F2) Ventral (F4 and F5).¹¹

2.1 F5: subpersonal visuomotor representations, goal relatedness and canonical neurons

The area called F5 occupies the most rostral part of the ventral premotor cortex. F5 neurons contain a distal hand and mouth movement representation (see Rizzolatti *et al.* 1981, 1988; Kurata and Tanji 1986).¹² F5 includes two large groups of neurons: the first is that of (A) *purely motor neurons*, whose activation is exclusively connected to actual movements. They constitute the overall majority of all F5 neurons, and belong to two kinds: (A1) neurons that fire whenever a movement is performed, and (A2) neurons that code only successful agent-object relationships, i.e., the achievement of a goal; for instance, grasping-related neurons fire whenever the monkey *successfully* grasps an object, regardless of the *effector* (i.e. the particular limb, or the particular organ employed) (see Rizzolatti *et al.* 1988; Rizzolatti, Fogassi, and Gallese 1999).¹³ Therefore these (A2) neurons in F5 are called *goal-related* neurons.

But there is also a second very interesting large group of neurons in F5, that of (B) *visuomotor neurons*: they have not only motor properties indistinguishable from those of the purely motor neurons, but also peculiar “visual” properties: in experimental tests the purely motor neurons fired during the grasp, while visuomotor neurons fired significantly also during the visualization, regardless whether a grasp followed or not. Visuomotor neurons are also distinguished in two groups: (B1) the so called *canonical neurons*, which discharge when an object is presented, even if no detectable action aimed at them is performed, either by the monkey or by the experimenter (Rizzolatti and Fadiga 1998; Rizzolatti, Fogassi, and Gallese 1999); (B2) the famous *mirror neurons*, which respond when the monkey observes an action performed by another individual, or when it performs the same or a similar action (Gallese *et al.* 1996; Rizzolatti *et al.* 1996).¹⁴

A fundamental functional property of area F5 is that most of its neurons do not encode *elementary movements* (like the mere extending of my arm), but *motor*

¹¹ Originally in Rizzolatti, Luppino and Matelli 1998: 285.

¹² Cited in Gallese and Metzinger 2003.

¹³ Cited in Gallese 2003: 1235.

¹⁴ Cited in Gallese 2003: 1236.

acts (or coordinated movements with specific purposes, like moving my arm in a specific direction to catch a glass) (Rizzolatti *et al.* 1988). The same elementary movement activating a neuron during a specific motor act (e.g., grasping) doesn't activate it during a different motor act (e.g., scratching). Thus, there are different groups of neurons in F5: grasping neurons, grasping-with-the-mouth neurons, hugging neurons, etc.

The activity of canonical neurons is characterized by “a strict congruence between their high selectivity for a particular type of prehension (executed grip) and the visual selectivity for objects that, although differing in shape, ... require the same type of prehension in order to be grasped” (Gallese 2000; Murata *et al.* 1997; Rizzolatti *et al.* 1988; Rizzolatti, Fogassi, and Gallese 1999).¹⁵ Imagine you have to grasp first a little box that can be contained inside your hand, and then a little stone: although their shape is different, these objects show the same affordance; therefore the motor acts satisfying this affordance (grasping the object with the whole hand) are the same.

In experiments with monkeys, just as the subject looks at the object its neurons fire, activating the motor program that *would be* involved were the observer actively interacting with the object. The evoked motor pattern remains just a potential act. Hence, the identification of an object is a preliminary form of action, a call to agency, characterized on the basis of its (visuo)motor opportunities, independently of whether an execution shall occur or not. This shows that in the recognition of objects agency and perception are two sides of the same coin: the sight guiding the hand is a kind of capacity to watch through the hand: the object that we perceive is encoded as a determined set of hypotheses of actions (Rizzolatti and Sinigaglia 2006: 44-47).

A very interesting result, correlated with the data described above is that mental action is a form of *neurophysiological simulation* of the physical action (Clark, Tremblay and Ste-Marie 2004). In particular, *motor imagery* and executed actions share similar physiological correlates (kinematic contents, dynamic changes in physiological parameters, functional anatomy). The (overt) execution of an action is necessarily preceded by its (covert) representation, but a (covert) representation is not necessarily followed by an (overt) execution of that action. This suggests that the representation “can actually be detached from execution and can exist on its own” (Jeannerod 2006: 2; see also Decety and Perani 1994; Decety and Ingvar 1990; Grafton *et al.* 1996; Johnson *et al.* 2002; Mühlau *et al.* 2005; Rumiati *et al.* 2004; Jeannerod 1994, 1997).

The activation of motor areas in representing an action provides the represented action with a ‘motor’ format, like the involvement of primary visual cortex in visual mental imagery restores the topographical layout of the image (see Kosslyn 1996, 2005). In order for a represented action to be felt as real, it needs to be framed within the constraints of a real action (Jeannerod 2001), so that it can be regarded by the motor system as the simulation¹⁶ of a real action. Thus, *motor imagery* is a *prototypical form of action representation*, or a *representation of evoked motor responses*, even though neural commands for muscular contractions are effectively present during motor imagery, but simultaneously blocked at

¹⁵ Cited in Gallese 2003: 1236; Gallese 2000: 31.

¹⁶ According to Metzinger (2003: 49-50), simulations are internal representations of possible properties of the world *in general*, while mental representations are the *special case* in which *actual* properties are simulated. See also footnotes 18 and 19 below.

some level of the motor system by an active inhibitory mechanisms (Jeannerod 2006). In other words, the fact that these representations can be regarded as simulations of real actions, shows that they have a motor format, i.e. a format framed within the constraints of the real action.

In § 2.2 and § 2.3 we shall see that the interdependence of motor and visual selectivity in canonical neurons is linked to representational mechanisms. This is an interesting kind of abstraction: looking at objects is unconsciously “simulating” a potential action; the *representation* of an object (based on the visualization of its affordance) is *integrated* with the ongoing simulation of the precise *potential* action which could be performed upon the object (Gallese 2000: 31). Hence, seeing an object is getting at the same time the *subpersonal visuomotor* (SV) representation of its affordance, and the internal *simulation* of one of the actions we could perform upon it (i.e. the most suitable motor program required to interact with it). In fact, SV representations, which are representations of those visual aspects of a target that are relevant to the action to be performed, *translate* the geometrical features of the target object into opportunities for action, and the visuomotor transformation mechanism converts visual information into motor commands of arm and hand movement towards the object (Jacob 2005: 248). Thus, this transformation mechanism reads the affordances as motor acts that can achieve one’s goal (see § 2.2 below).

Furthermore, these SV representations allow us, as we perceive an object, to automatically compute the most suitable motor act that could be performed on it for some purpose (say, the way I can grasp it: Butterfill and Sinigaglia 2012; Jacob and Jeannerod 2003; Jeannerod 2006). This idea of motor simulation¹⁷ has been proposed as a general framework for motor cognition, as the

¹⁷ For neurophysiological technical details and a more accurate philosophical distinction between the concept of motor simulation and that of motor representation, see Jeannerod 2006, Ch. 2 “Imagined Actions as a Prototypical Form of Action Representation”, and Ch. 6 “The Simulation Hypothesis of Motor Cognition”. His data show that motor activation is highly specific to the action that is represented. Both forming motor images and observing other people acting involve motor cortex, premotor cortex, SMA, the basal ganglia and the cerebellum, i.e. the main neural structures which are needed in executing actions (here however we cannot discuss simulation in the case of mirror mechanisms and mirror neurons processes). For a review see Jeannerod 1994, 1997, 2001, 2006; Decety and Ingvar 1990; Hommel *et al.* 2001: 860. What differentiates Jeannerod’s proposal from the others is that according to him: “We do agree that actions are represented in terms of their goal: but we assume that the goal is only part of the content of the action representation. By representing the goal, we can answer the question of ‘What the action is about’, but not the question of ‘How to do it’. The latter question requires motor simulation to be answered (and we saw how important it may be to answer it for mentally rehearsing an action or learning it by observation)” (Jeannerod 2006: 134). Furthermore, an interesting philosophical analysis concerning the concept of simulation is offered by Metzinger 2003, according to which mental representation is a *special case* of mental simulation: simulations are internal representations of possible properties of the world. Representations, instead, concern actual properties of the world (49-50). Here mental simulation is a form of internalized *motor behaviour* and can be compared to goal-representing states. Empirical frameworks very similar to this have been proposed, but they understand simulation as an *internal forward model of motor* consequences (Wolpert *et al.*, 1995; Wolpert 1997; Kawato 1997, 1999; Grush 2004), or as prediction (Friston 2009; Clark 2013). For further interesting discussions see Leopold, Logothetis 1999; Kukla 1992: 222.

basic mechanism for explaining the functioning of motor representations¹⁸. Simulation is what makes it possible to activate perceptual mechanisms in the absence of a stimulus, or to activate motor mechanisms without executing an action. “If motor cognition is based on simulation of our own actions, and if the mechanisms each individual uses to simulate his own actions is the same as that other individuals use, as we have good reason to believe, then we can develop the idea that perceiving and producing actions are the two faces of the same process [...]. If the assumption that represented actions correspond to covert, quasi-executed actions is correct, then represented actions should involve a simulation of the mechanisms that normally participate in the various stages of action generation, including motor execution” (Jeannerod 2006: 130-31).

It should be noticed that what takes place in F5 can be easily described through the concept of representations, and “through the idea of a crystallization of motor codes as stable functional units within the brain. Since the movements codified in the abovementioned cortical areas have a somatotopic organization in the motor system¹⁹, and the stimulation of the same cortical site always produces the same complex response, it is natural to conceive the cortical activity in those sites as representations of those evoked motor responses. In other words, each particular site includes a series of spatial and temporal directives. For instance, the area concerned with grasping and taking to the mouth includes directives about which muscles of the hand, wrist, arm and mouth must be contracted, and when” (Caruana and Borghi 2013). And all this is controlled by the *visuomotor transformations* happening in AIP-F5 (discussed in § 2.2 below).

Thus it seems to us that empirical evidence is best interpreted by models in which representations play a role in natural cognitive systems. This however is more a methodological or epistemological hypothesis on how to do cognitive science, than a metaphysical claim, which at least for the time being we cautiously prefer to avoid.²⁰

¹⁸ “This is not to say that activation of the motor system is the same during simulation (in its various forms) as during execution and various forms of simulation: simulating is not doing, and substantial differences are observed between simulation and execution. First, the activation of most of the areas of the motor system during action representation is consistently weaker than during execution. Secondly, it is coupled with an additional mechanism for suppressing motor output, a prerequisite for the off-line functioning of the representation. Thirdly, because the muscles do not contract and the limbs do not move, the sensory reafferences normally produced by a movement are lacking. These differences are sufficient to disentangle simulating from doing. However, the representations for executing and simulating do not completely overlap, which may allow this distinction to be made even in the absence of sensory reafferences” (Jeannerod 2006: 131).

¹⁹ I.e., groups of neurons related to adjacent parts of the body are themselves adjacent, so that the control of the movement of different parts of the body is centered in specific regions of the cortex.

²⁰ Chemero (2000) calls respectively ‘Nature hypothesis’ and ‘Knowledge hypothesis’ what we have called here “epistemological hypothesis” and “metaphysical claim”: “The main difference between the nature and knowledge hypotheses can be put as follows: the knowledge hypothesis is to a much greater extent a (*meta*)scientific hypothesis. That is, the knowledge hypothesis concerns how we ought to do cognitive science, whatever the mind is really like. The nature hypothesis, on the other hand, is to a much greater extent a *philosophical* hypothesis; it concerns what the same region of the world (cognitive agents) is really like, however that region is best explained scientifically” (Chemero 2000).

2.2 AIP-F5, Affordances, and Enactivism

Area F5 is highly connected and interacts with the anterior intraparietal area (AIP), whose neurons are activated during hand movements. We can call this unified system AIP-F5.²¹ AIP-F5 involves the visuomotor transformations necessary to grasp an object (Sakata *et al.* 1995; Murata *et al.* 2000).²² AIP-F5 neurons are selectively responsive to tridimensional stimuli, so supporting Gibson's intuition: the visualization of the object and the related affordances activate neural groups in AIP. Visual information is first elaborated in AIP, then it passes over to F5 visuomotor canonical neurons, which don't encode the individual affordances already visualized in AIP, but the potential motor acts congruent with them. Thus, F5 allows to act upon the object, selecting the best motor behaviour thanks to the previous visual information based on the affordances. The selected action does not depend only on the intrinsic properties of the object, but also on the use we make of it and its purpose (Rizzolatti and Sinigaglia 2006: 35-36). Visual information is then translated into motor information and sent into F1, the region involved in action execution. AIP-F5 is the cortical portion in which the visuomotor transformations occur. The link between AIP and F5 is much more complex than we describe here, but the details we offer here are sufficient in order to make our philosophical point. For a complete review of their activity in line with computational neuroscience and studies on single cell recordings see Chinellato and del Pobil 2015, Borghi and Riggio 2015; for an overview of the cortical areas which are very akin to the AIP-F5 circuit see Turella and Lignau 2014.

The set of actions and motor behaviours we can perform in the environment is thus inscribed into the cortex: every object offers several affordances, hence several possible ways of acting upon it. However, each time we exploit just a small set of these possibilities. Indeed, during our ontogenetic development, the pruning of our neural networks under the pressure of experience selects in F5 the few neural populations linked to the most effective motor acts. This learning mechanism is called "motor reinforcement". Thanks to this functional selection our cortex structures a sort of *motor vocabulary* (see below) that facilitates the combination between the motor acts encoded by F5 and the visual affordances abstracted in AIP (Rizzolatti and Sinigaglia 2006: 45).²³

This is further confirmed by more recent empirical evidences:²⁴ concerning the motor functions of the parietal lobe, Fogassi and Luppino (2005) reported new data confirming the general consensus that the posterior parietal cortex is part of the motor system and plays a fundamental role in visuomotor transformations. Bonini *et al.* 2014 show the leading role of the supplementary motor area (SMA) in the capacity to evaluate the outcomes of our actions; this capacity is fundamental for adapting and optimizing behaviour and depends on an ac-

For this debate see Chemero 2000, 2009; Hutto 2013; van Gelder 1995, 1998; Dennett 1987; Brooks 1991, 1999; Clark and Toribio 1994).

²¹ See also Castiello 2005.

²² Cited in Rizzolatti and Sinigaglia 2006.

²³ Here we cannot deal with the so called *non-inferentiality* of perception, although a comparison might be fruitful: see Zipoli Caiani 2013a; Noë 2004; Rizzolatti and Sinigaglia 2006.

²⁴ We are grateful to an anonymous referee for calling our attention to this topic.

tion-monitoring system that assesses ongoing actions and detects errors and rapidly evaluates successful and erroneous actions.

Raos *et al.* (2006) further investigated the motor and visual properties of F5 grasping neurons, using a controlled paradigm that allows the study of the neuronal discharge during both observation and grasping of many different three-dimensional objects, with and without visual guidance. Hierarchical cluster analysis indicated that the selectivity of both the motor and the visual discharge of the F5 neurons is determined not by the shape of the object, but by the grip posture used to grasp the object. All neurons displayed a *preference* for grasping of a particular object or set of objects.²⁵ The same preference was maintained when grasping was performed in the dark without visual feedback. In addition to the motor-related discharge, about half of the neurons also responded to the presentation of an object or a set of objects, even when a grasping movement was not required. Often the object evoking the strongest activity during grasping also evoked optimal activity during its visual presentation. Because the same paradigm has been used to study the properties of hand-grasping neurons in the dorsal premotor area F2 and in the anterior intraparietal area (AIP), these authors have been the first to compare the functional properties of grasping-related neurons in the three cortical areas (F5, F2, AIP).

Baumann, Fluet, and Scherberger (2009) provide compelling evidence that while a macaque is planning to grasp a single object (a handle), neurons in its parietal area involved in hand preshaping simultaneously encode multiple potential grasp movements before one is chosen for action. Other recent studies on affordances and motor system also confirm that F5 and AIP form a frontoparietal network for transforming visual signals into hand grasping instructions (Brochier and Umiltà, 2007; Brochier *et al.* 2004). Besides, these areas represent upcoming hand movements at a conceptual or categorical level (Townsend, Subasi, and Scherberger 2011) well before their execution (Raos *et al.* 2006; Baumann, Fluet, and Scherberger 2009; Fluet, Baumann, and Scherberger 2010; Townsend, Subasi, and Scherberger 2011).

Despite the fact that a single object can afford multiple types of grip, depending on the intended goal, so far studies have examined AIP neural activity only in monkeys trained to perform a single type of grip on a particular object. While the simplicity of such tasks has largely revealed the functional importance of AIP in grasping, the context and circumstances of everyday situations demand more flexibility in the selection of types of grip, and the role of AIP in facilitating such flexibility has remained unexamined. Hand grasping requires the transformation of sensory signals to hand movements. Neurons in area F5 (ventral premotor cortex) represent specific grasp movements (e.g., precision grip) as well as object features like orientation, and are involved in movement preparation and execution.

Fluet, Baumann and Scherberger (2010) examined how F5 neurons represent context-dependent grasping actions in macaques. Their results reveal important differences in how grip type and object orientation are processed in F5, and suggest that anatomically and functionally separable cell classes collaborate to generate hand grasping commands. The same authors addressed this issue by investigating AIP neural activity during a delayed grasping task in which monkeys were cued to grasp a handle at one of five different orientations, using ei-

²⁵ I.e., they preferentially fire in front of that object or set of objects.

ther a precision or a power grasp (Baumann, Fluet and Scherberger 2009). When handle orientation and grip type information were concurrently presented, AIP neurons showed sensitivity to handle orientation, grip type, or both, and could be classified according to their tuning onset (planning vs. movement execution) (ibi, Fig. 2A-C; see also Gallivan and Wood 2009). In order to perform grasping movements, the hand is shaped according to the form of the target object and the intended manipulation, which in turn depends on the context of the action. The anterior intraparietal cortex (AIP) is strongly involved in the sensorimotor transformation of grasping movements, but the extent to which it encodes context-specific information for hand grasping is unclear. Baumann, Fluet, and Scherberger (2009) showed that, in a cue separation task, when the object was presented first, neurons representing power or precision grips were activated simultaneously until the actual grip type was instructed. In contrast, when the grasp type instruction was presented before the object, type information was only weakly represented in AIP, but was strongly encoded after the grasp target was revealed. We conclude that AIP encodes context-specific hand grasping movements toward perceived objects, but in the absence of a grasp target, the encoding of context information is weak.

Some studies examined in detail the tuning properties of single units in both AIP (Sakata *et al.* 1995; Murata *et al.* 2000; Baumann, Fluet and Scherberger 2009) and F5 (Rizzolatti *et al.* 1988; Fluet, Baumann and Scherberger 2010). Besides, it has been showed that neural activity in F5 is better suited for the decoding of the grip type, while in AIP it is more accurate in predicting object orientation (Baumann, Fluet and Scherberger 2009; Fluet, Baumann and Scherberger 2010). The experimental evidence we reported about the AIP-F5 circuit concerns both human and non-human primates, and the correspondences between the respective cortical areas have been studied in the literature (see Borghi and Riggio 2015: 3; Shikata 2003).

AIP-F5 neural activity represents more than just a confirmation of Gibsonian and enactivist intuitions about the UAP and the related sensorimotor activity at cognitive level: it also constitutes a neural correlate of the UAP and affordances in the cortex on which the cognitive level depends. Moreover, in literature there is no agreement on whether the epistemic portion of affordances, which clearly depends on the subject, is to be classified as personal or subpersonal, or both; but AIP-F5 activity shows that affordances certainly play a role at subpersonal level (whether or not it also emerges at personal level).

That visuomotor canonical neurons have both visual and motor selectivity shows precisely that sensory phenomena involve motor neural mechanisms, while the premotor cortex has an important visual component: object recognition is possible thanks to F5 motor “vocabulary”, which is the basis of the cognitive functions commonly attributed to the sensory system. For instance, take the following sequence: (i) I am thirsty. So, when (ii) I see a glass of water, (iii) I realize that I can satisfy my thirst by catching it, hence, (iv) I get ready to act accordingly. Well, the remarkable thing is that, thanks to the visuomotor transformation mechanisms, (ii) and (iii) (the affordances) and (iv) (the motor act) are all encoded in the same circuit, that is, AIP-F5, and activated by the firing of the same neural populations.

Empirical evidences confirm UAP in two ways. First, as said, the motor cortex is basic for sensory and perceptual processes (§ 2). In particular, recognizing the affordability of an object crucially involves (beside the visual dorsal

pathway) also the ventral premotor cortex. This means that sensory information is directly mapped on motor areas, so allowing us to perceive the environment in terms of possible motor acts.

For instance, an automatic process of grip formation takes place during the transportation of the hand: as we mentioned, the fingers are preshaped much before the hand touches the object.²⁶ Transportation of the hand itself involves initially a progressive opening, and then a closure of the fingers. This movement is completely automatic and subpersonal, and at about 60% of its transportation the hand reaches its widest opening, or *maximum grip aperture* (henceforth: MGA). It has been found that the size of the finger-grip at MGA (though much larger than the object to be grasped) is linearly correlated with the size of the object. This shows that the calibration of the finger-grip aperture is made automatically on the basis of a SV representations of the geometrical properties of the object (Jeannerod 2006; Jacob and Jeannerod 2003). “Thus, motor commands are generated such that the corresponding arm, hand and finger movements match the geometrical properties of the object to be grasped and handled (its location, size, shape and orientation). Simply observing the grasping hand reveals that this process is largely anticipatory and pertains to an action representation, not to a mere on-line adaptation of the motor commands to the object” (Jeannerod 2006: 5).

Actually, a very interesting proposal to model affordance perception in a dynamical anti-representationalist approach has been offered by Chemero (2009, § 7.6). However, the account based on representations has proven epistemologically²¹ more fruitful in understanding how affordances are perceived. Moreover, data on AIP-F5, which provide the best available explication of these processes, are never mentioned by the radicalist accounts. We think that challenging the representational stance would be challenging those data.

Moreover, this already suggests that canonical neurons have a representational nature: for, how can the hand take the right aperture before reaching the object, unless it is guided by a representation of the object codified in its motor system? Thus, even though apparently the empirical data in cognitive neuroscience can be interpreted both from a representational and a non-representational point of view (Gallagher 2008, Hutto 2005; Hutto and Myin 2013), in this precise empirical framework it seems they do not admit of an equally good interpretation from the two perspectives: for both affordances and canonical neurons (and in general the cognitive processes occurring thanks to the dorsal visual stream and the AIP-F5 area) are better and more fruitfully interpreted in a representational framework (Jacob and Jeannerod 2003). Furthermore, as mentioned in the Introduction, while the literature on enactivism usually cites Milner and Goodale’s two-visual-systems model, it never mentions the empirical evidences concerning the AIP-F5 cortical circuit.²⁷

²⁶ Baumann *et al.* 2009 provide compelling evidence that during grasp planning toward a single object (a handle), neurons in a macaque parietal area involved in hand preshaping simultaneously encode multiple potential grasp movements before one is chosen for action.

²⁷ Actually Noë has been criticized by Hutto (2005) for failing to take into account subpersonal representations. But Hutto’s argument—explained in (Menary 2006)—is purely philosophical, and it does not report any empirical data. Also Gallese and Keysers claimed that “Positing the importance of sensorimotor contingencies for perception is by no means denying the presence and importance of [subpersonal] representations”

The second kind of empirical evidences confirming UAP concerns the functional linkage between perception and action discussed in the literature about disorders due to cortical lesions. As said, evidences showed that the dorsal visual pathway (the pragmatic pathway of vision for action)²⁸ links the primary visual cortex (V1) to the (posterior) parietal lobe, hence to the AIP-F5 circuit. The latter automatically transforms the visual information about the properties of objects into motor commands, responding to those 3D geometrical properties of objects that serve such visuomotor tasks as grasping them (Milner and Goodale 1995; Matelli, Luppino and Rizzolatti 1985; Castiello 2005; Jacob and Jeannerod 2003).

Certain lesions in the dorsal pathway damage the visuomotor transformation process, causing impairments in spatial orientation and in the ability to localize objects in space; in such cases patients can still perceive and recognize objects, but they fail to grasp them normally, even though no disease occurs in the motor cortex (Milner and Goodale 1995, 2004; Ungerleider and Mishkin 1982; Gangopadhyay, Madary and Spencer 2010; Fridland 2012).

Indeed, posterior parietal lesions can cause optic ataxia, a deep alteration of reaching movements directed towards a visual target, in the absence of any motor impairment (Jacob, Jeannerod 2003; Jeannerod 2006). Three phenomena are observed in such cases: first, the kinematics of the movements is altered, since they have a lower peak velocity and the duration of their deceleration phase is increased. Such a deficit cannot have a motor origin, since the same movements can be executed with a normal kinematic profile in non-visual conditions. Second, the movements are not properly directed towards the target—their directional coding is impaired—and large pointing and reaching errors are observed (e.g., Milner *et al.* 1999). Third, alteration of the movements is not limited to the reaching phase. Distal aspects of the movements are affected as well. During the action of grasping an object, the finger grip aperture is increased, and the usual correlation between MGA and object size is lost (Jeannerod 1986). Similarly, optic ataxic patients fail to orient their hand properly when they have to insert an object through an oriented slit (Perenin and Vighetto 1988).

Optic ataxia appears to be a disorder limited to transforming visual properties of objects into motor commands for a hand action directed towards these objects. It is not due to misperception of the shape, orientation or size of the objects (see also Jeannerod *et al.* 1994; Goodale *et al.* 1994). Moreover, patients with parietal lesions, with or without optic ataxia, often present visuospatial disorders.

(Gallese and Keysers 2001: 983). They used findings about mirror neurons (see § 2.1 and § 2.2) to show “the intrinsic relationship between action control and representation within the logic of forward models” (Gallese and Keysers 2001: 983). However, their data are different from ours, as they concern a different (although similar) kind of neurons. Moreover, they do not enter into the kind of considerations we develop in § 3.

²⁸ According to Milner and Goodale’s (1995) famous two visual systems theory, the ventral stream of visual processing is responsible for conscious qualitative perceptual experience, while the dorsal stream is responsible for the fine-grained motor coordination required for action instantiation. Milner and Goodale claim that the two streams interact insofar as the ventral stream selects the goals for action and the dorsal stream carries out the movements required for satisfying these goals. As noticed in footnote 6, of course, not all visual perception is aimed to action.

2.3 Words and representations in the brain

It has been pointed out (Rizzolatti *et al.* 1988) that F5 represents a *vocabulary*, in which motor acts are inscribed, each “*word*” being constituted by a group of neurons, each of which refers to, or represents, one kind of *motor act* (rather than simple *movements*).

The referent of these “words” can be of different generality: for instance, the general goal of the action (e.g., in goal related neurons: grasping, holding, tearing), or the particular way in which it must be executed (e.g., in visuomotor neurons: *precision grip*, by the index finger and the thumb) (Gallese and Metzinger 2003: 367). So, these “words” work as general terms, referring to *kinds*, rather than particulars (Caruana and Borghi 2013): as far as F5 is concerned, the cortex ignores the single movements whose sequence makes up the act (like, e.g. flexing the thumb, extending the index, etc.): the motor act is represented as a whole, and directly selected by activating the related neural population (Gallese and Metzinger 2003: 367-68). There is a clear computational advantage, here, due to the “motor reinforcement” mentioned in § 2.2, which during ontogenetic development selects representations of the more effective motor acts.

Grasping acts are executed under visual guidance: there is a relationship between the 3D visual features of objects and the specific “words” of the vocabulary. For instance, seeing an object and wanting to grasp it evokes a command to grasp by a specifically suitable finger configuration. Thanks to the motor “vocabulary” the appearance of the graspable object in the visual space will immediately retrieve the description codifying the appropriate motor act. So the classification of the objects as to their visual aspects corresponds to the classification of the acts we can perform upon them recorded in the motor vocabulary: the cortical integration of vision and action generates and controls goal-related behaviours by producing internal copies of actions.

Thus subpersonal representations are at the basis of our motor skills to handle sensorimotor contingencies. Our sensorimotor behaviour does not result from the operation of two separate modules (vision and tact) which interact only at the cognitive level: they are already integrated at the level of cortical representations. So, subpersonal representations are fundamental for the intentional stance that characterizes our relation with the external objects.

As mentioned in § 1, according to Noë “We ought to reject the idea that the perceptual system constructs an internal representation of the world” (Noë 2004: 2). On the other hand, “No doubt perception depends on what takes place in the brain, and very likely there are internal representations in the brain” (*ibi*).

These quotes might seem contradictory, but they would be consistent if Noë were talking of representations in two different senses. Noë does not explain which kind of representations he is thinking about²⁹, but at least two reasonable hypotheses can be advanced. First, that Noë is concerned with rejecting “propositional” representations, in the sense in which cognitivists like Fodor have claimed that basic cognition relies on propositional attitudes; in other words, what he rejects are propositional representations which consist in a sort

²⁹ Noë and Thompson (2004: 4) focus on the question about the neural correlates of consciousness (NCC). However, they mainly discuss whether or not “neural states that have been shown experimentally to be correlated with conscious visual experiences match those experiences in content”.

of amodal, disembodied *mental gymnastic* (Fodor 1975, 1978; for a review see Hutto 2005, Hutto and Myin 2013; Menary 2006; Noë 2002, 2004).³⁰

The second hypothesis is that, as mentioned in § 1, he rejects only “snapshot representational pictures”, that is, *pictorial* representations which “represent the whole scene in consciousness all at once in the way a photograph does”, such as those involved in Marr’s account of vision (Marr 1982).

But the representations we are concerned with are of neither kind: first, our SV representations are a particular form of representational mechanism arising from visuomotor transformation processes occurring in AIP-F5. So, it might be pointed out that since SV representations have a motor format,³¹ they are non-conceptual and non-propositional (Evans 1982; Heck 2000; Peacocke 2001; McDowell 1994), contrary to classical representations (Fodor 1983, 1989, Fodor and Pylyshyn 1988). In fact, the “computation” by which their motor format is realized does not process propositions, or anything that can be true or false (like, e.g., the claim that an object exists), but just parameters: some particular spatial features translated as commands for a motor act.³² For instance, it is the computation of the particular way in which an act can be executed with respect to, say, a small, tapered, thin object; that is, in this case, by a precision grip. As they put it in the literature, what is computed is the suitability of a potential motor act to operate upon what we find in the external world (Butterfill and Sinigaglia 2012; Jacob and Jeannerod 2003; Jeannerod 2006). The process of motor representation allows to functionally overcome the distinction between perception and action: in fact, through SV representations and the visuomotor transformation process by which they are subserved, the brain represents how the perceptual features of objects must be read as contents of a motor nature (precisely, of a sensorimotor nature: e.g., action goal, a precise grasp to perform). Indeed, the output of the motor processing of visual stimuli is ‘motorically’ encapsulated (Jacob and Jeannerod 2003: 177).³³ Hence, the motor representations can be defined as an internal state of the subject in which perception and action are not precisely delimited (Jeannerod 2006). Obviously, the vehicle of these representations is, in general terms, the entire pathway that goes from the primary visual cortex (V1), through the dorsal visual stream ending to the (posterior) parietal lobe, hence to the AIP-F5 circuit: i.e., the complex of the cortical sites described in this section.³⁴

In particular, these representations are not inferential or propositional representations, such as those involved in the *language of thought hypothesis* (or *mentales*) (Fodor 1975, 1978), nor they are amodal or disembodied, as they are developed through motor reinforcement (see § 2.2). Moreover, our representations are not “snapshot representational pictures”, since they do not represent “the whole scene in consciousness all at once in the way a photograph does”. On the

³⁰ We owe this suggestion to an anonymous referee.

³¹ See § 2.1, § 2.2.

³² Indeed, both hand preshaping and SV representations are automatic processes. In fact, the dorsal stream of visual processing grounding the perception of affordances is almost totally independent from conscious phenomena. For further technical details, see Jeannerod 2006; Jacob and Jeannerod 2003. For a complete account of how the AIP-F5 circuit constructs perceptual representations which are not structured in a propositional format, see Ferretti, forthcoming-a.

³³ See § 2.1, § 2.2, § 2.3 above.

³⁴ Further technical details have already been given at § 2.1, § 2.2.

contrary, since they are constituted by “words”, they codify only some selected features of objects, like 3D structure, and some corresponding features of actions, like goals or types of prehension.

Therefore, there need be no contradiction between Noë’s rejection of “propositional” and/or “snapshot” representations, and our claim that there are non-conceptual, non-propositional, SV representations at the cortical level.

3. Is perception direct in the light of UAP and Affordances?

As mentioned in the beginning, on the basis of UAP and the relative use of affordances (claim E1) enactivists claim that perception is direct (E2). In order to assess the latter claim, however, some conceptual clarification is needed.

There are at least 3 things one could mean by the claim that perception is direct:

- 1) That no representation at all is constructed or involved in perception, whether conscious or unconscious, at the personal or subpersonal level, pictorial or propositional.
- 2) That there is no “snapshot”, no pictorial representation of the whole scene in all its details all at once as a photograph, at least at the personal level (as claimed by Noë), or even at the subpersonal level.
- 3) That perception *appears* direct, i.e. we have no conscience of any representation mediating between the object and our perception of it.

These claims are in order of decreasing strength: (3) might be true even if (2) is false, and (2) might be true even if (1) is false. In fact, there is no question that (3) is true, and we are ready to grant (2) as well. But the evidence described in § 2 abundantly shows that (1) is false: first-person experience stands on the basis of the SV representations, thanks to which we can be aware of objects and “catch” them (both cognitively and physically). Moreover, in spite of the truth of (2) and (3), any simple claim to the effect that “perception is direct” without further qualifications would be seriously misleading, for it would risk to conflate (2) and (3) with (1). Of course one may decide to understand ‘direct’ in sense (2) and/or (3), as apparently the enactivists tend to do; but this terminology would not be very useful; in fact, it might be misleading, given the crucial role played by neural representations: it is thank to them that objects *appear* as directly given at the phenomenal level.

As mentioned, enactivists hold that E1 (the doctrine of affordances and UAP, action-perception union) entails E2 (that perception is direct). In so doing, they cannot mean ‘direct’ but in senses (2) or (3). On the other hand, E1 could hardly be credible if we didn’t understand how it is implemented at the neural level. But the empirical findings discussed here precisely show how this implementation occurs and what the neural correlates of UAP and affordances are. In particular, we have seen that the integration of perception and action does not happen at the cognitive level, but already at the cortical level. Just for this reason, however, perception is *not* direct in sense (1). So, experimental evidence shows that claim, E1, hence also E2, are not compatible with (1): in a very important sense, direct perception is *not* possible in the light of UAP and affordances.

Conceptual confusion might also derive from the claim that

(4) perception is transparent,³⁵

and the ensuing argument that

(5) perception is direct *because* it is transparent.

In fact, (4) suffers the same kind of ambiguity as the claim that perception is direct: on the one hand, (4) might mean that we cannot perceive any representation between us and the object,³⁶ i.e., that perception *appears* direct; in this case (4) would be synonymous of (3), and (5) would be valid, but tautological.

On the other hand, we can properly call “*trans-parent*” only what is positioned between a subject and an object, but through which one can see, like a glass, a lens, the atmosphere, etc. One of these mediums is called transparent when (i) it cannot be noticed, and/or (ii) it does not prevent or significantly distort our perception of the object. In this particular case, we are not talking of a physical medium standing between our body and the external object, but of the neural visuomotor representations in F5 which mediate between the physical inputs from the object and our perception at personal level. Now, these representations are transparent precisely in both senses, since (i) the subject is unaware of them, for they do not surface at the personal level,³⁷ and (ii) they do not prevent or distort perception (in fact, they constitute its physical realization).

So, the most proper way of phrasing (4) would be saying that perception happens through transparent hidden representations. And this of course would entail both (3) and the negation of (1). In other words, perception involves sub-personal representations, so it is indirect in a relevant (perhaps the *most* relevant) sense of the term.

On the other hand, as explained by Metzinger, perception is no longer transparent in the case of hallucinations: “if an hallucination is occurring, I am no longer looking “through” (in the sense of thanks to) the state in my head on-to the world, but only at the representational vehicle itself—without realizing *this fact*” (Metzinger 2003: 173).*

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³⁵ E.g.: “The transparency, or diaphanousness, of experience poses a problem for the theory of perception. To describe sensory experience, to reflect on it, is to turn one’s attention to the experienced world. The experience itself is transparent” (Noë 2004).

³⁶ E.g., “There’s only encountering the world content as you experience it. It would seem, then, that we cannot reflect on experience itself” (Noë 2004).

³⁷ Gallese and Metzinger 2003: 370.

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