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Seeing with the hands

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When witnessing someone else's action people often take advantage of the same motor cognition that is crucial to successfully perform that action themselves. But how deeply is motor cognition involved in understanding another's action? Can it be selectively modulated by either the agent's or the witness's being actually in the position to act? If this is the case, what does such modulation imply for one's making sense of others? The paper aims to tackle these issues by introducing and discussing a series of experimental studies showing how body and space may constrain one's own motor cognition reuse in understanding another's action. These findings, I shall argue, may shed new light on the mechanisms underlying the primary ways of identifying ourselves with other people and of being connected to them.

Keywords: motor cognition; social cognition; space representation; mirror neurons; proactive gaze

1. Introduction

When witnessing someone else's action people often take advantage of the same motor cognition that is crucial to successfully perform that action themselves. Active or former football players are likely to watch a match very differently from people who don't have any football competence at all, being the former, but not the latter, able to immediately make sense of various players' moves. But this holds not only for high-level skilful activities such as playing football or the violin, but also for very basic actions like grasping a cup of tea or throwing a stone into the lake.

The discovery of mirror neurons in the macaque monkey brain (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996) and evidence for the existence of a mirror mechanism in humans (Fadiga et al. 1995; Rizzolatti et al. 1996; Grafton et al. 1996) provided a neuronal mechanism to account for the role of one's own motor cognition in others' action processing, by showing that both executing and witnessing a given action may recruit the same fronto-parietal motor areas (Rizzolatti et al. 2001;

Rizzolatti & Sinigaglia 2008). When witnessing another's action, this cortical motor recruitment would allow a direct matching of the sensory to the motor representation of that action, thus enabling the witness to immediately understand what another individual is doing (Rizzolatti & Sinigaglia 2010; Sinigaglia 2010).

But how deeply is motor cognition involved in understanding another's action? Though the neuronal underpinnings of motor-based making sense of others has been largely investigated over the last few years (see for a review Gallese et al. 2009; Gallese & Sinigaglia 2011), little research has been explicitly devoted to highlighting to what extent people can really reuse their own motor cognition in witnessing someone else acting. More specifically, can this motor cognition reuse be selectively modulated by either the agent's or the witness's being actually in the position to act? Can such modulation be also related to the range of the witness's space representation? If this is the case, to what extent can the motor cognition reuse be space-dependent and what does such dependence imply for one's making sense of others?

The present paper aims to tackle these issues. There are three sections to come. In the first section, I shall briefly sketch the functional properties of the mirror mechanism, focussing on its role in action understanding. In the second section, I shall introduce and discuss a recent series of experimental studies investigating how body and space may constrain the mirror mechanism recruitment and therefore the motor cognition reuse as measured by the proactivity of the witness's gaze. Finally, in the third section, I shall delve into the spatial constraints of the mirror-based motor cognition reuse, by arguing that the account of such constraints may shed new light on the mechanisms underlying the primary ways of identifying ourselves with other people and of being connected to them.

2. Understanding actions from the inside

Single cell recordings from the ventral premotor cortex (area F5) and from the inferior parietal lobule (areas PF/PFG and AIP) of macaque monkeys revealed the existence of a set of motor neurons (mirror neurons) becoming active both during the execution and the observation of goal-directed movements (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996; Gallese et al. 2002; Fogassi et al. 2005; Rozzi et al. 2008). For the first time a neural mechanism transforming the sensory representation of an action into the motor representation of that action was identified. This sensory-motor transformation goes beyond the mere kinematic features of action, since it occurs at the level of the motor goal-relatedness shared by the actively executed and the partially seen (Umiltà et al. 2001) or heard (Kohler et al. 2002) action. In addition, F5 mirror neurons selectively respond when executing and witnessing a given motor act such as grasping objects regardless of the effector (hand or pliers) and the sequence of

movements (opening or closing the fingers) required to accomplish the goal (Rochat et al. 2010).

Neurophysiological and brain imaging studies demonstrated that witnessing someone else performing a given action recruits in humans the same premotor and parietal areas as if executing that action (for review, see Rizzolatti et al. 2001; Rizzolatti & Sinigaglia 2010), being such recruitment strictly correlated to the witness's motor expertise (Calvo Merino et al. 2005, 2006; Cross et al. 2006; Haslinger et al. 2006; Aglioti et al. 2008). The human parieto-premotor mirror mechanism is also selective to motor goals when relying on action sounds (Lewis et al. 2005; Gazzola et al. 2006). A similar functional property was also evident in congenitally blind patients (Ricciardi et al. 2009).

Finally, experiments carried out in monkeys (Fogassi et al. 2005; Bonini et al. 2009) and humans (Iacoboni et al. 2005; Cattaneo et al. 2007; Ortigue et al. 2010) showed that the mirror mechanism also maps basic motor intentions, enabling one to represent the witnessed action (e.g. grasping) in terms of its final goal (grasping something for eating or for putting it away).

But why should one's motor areas be recruited when witnessing someone else acting? And why should this recruitment be selective to motor goals and intentions? Ever since its discovery, the mirror mechanism has been argued to subserve action understanding (di Pellegrino et al. 1992; Rizzolatti et al. 1996; Gallese et al. 1996). Witnessing other people performing a given action elicits a motor activation in the witness's brain as if she planned and executed that action herself. The witness can thereby take advantage of her own motor cognition in making sense of other people, thus immediately grabbing the motor goal and the motor intention of their action without any inferential processing (Rizzolatti et al. 2001; Rizzolatti & Sinigaglia 2008).

Of course, claiming that the mirror mechanism may play a role in understanding what other people are doing is not tantamount to claiming that this is the only way to fulfill this function. Indeed, according to many authors, understanding other people's actions amounts to reading their mind, that is, to attributing to them mental states, such as beliefs and desires, that can be construed as putative reasons for their actions (Carruthers & Smith 1996; Goldman 2006; Hutto & Ratcliffe 2007). Furthermore, action understanding may sometimes rely even on a mere associative mechanism allowing one to link two (or more) stimuli to one another in virtue of their simple covariation.

What is so special with the mirror-based action understanding is that one may understand other people just by means of the same motor cognition that enables her to successfully perform that action. Take the case of a skiing instructor who is often in the mood for jokes. From time to time, he likes to deceive his students by performing bodily movements that, although compatible with the demonstrated action, are not the most appropriate ones. You are an absolute beginner, while your friend Peter is a

very good skier. That the instructor is doing something strange will be immediately understood by Peter, who will ask the instructor what this bizarre movement is for, while you will be unable to recognize whether the instructor's movement is appropriate or not.

It is his skiing ability that allows Peter to understand the instructor's behaviour. Such understanding, however, is not grounded in a mere associative mechanism nor does it imply any explicit mentalizing. There is no reason to assume that you are less able than your friend to read the mind of the instructor by meta-representing him as having certain propositional attitudes in order to account for the fact that you cannot actually understand *what* the instructor is really doing. Nor is there any reason to assume that your friend is used to attending to skiing instructors who like joking. What counts here is the ability to understand the goal-relatedness of another's movements on the basis of one's own motor cognition.

Elsewhere I called this kind of understanding an "understanding from the inside" (Rizzolatti & Sinigaglia 2010; Rizzolatti & Sinigaglia 2011), meaning thereby that one may grasp what other people are doing by exploiting what she can do, that is, her own action possibilities. The richer are these action possibilities the greater is the sensitivity to other people's actions, shaping the ability to act and the ability to make sense of others to the extent that the latter can be construed in terms of the former (Sinigaglia 2009; on this point see also Rietveld in this volume).

To this regard, it is worth noting that mirror-based action understanding not only unifies witnessed and executed actions, considered as two stages of the same continuum (Jeannerod 2001, 2003), but also ends up undermining the sharp distinction between observational and engaged stance. It is here crucial to avoid confusing the experimental setting of earlier mirror experiments with the function of the mirror mechanism. Mirror investigations usually attempted to decouple the acting and witnessing phases, because this was the only way in which the motor responses when witnessing other people's actions could be convincingly labelled as "mirror". But this does not imply that mirror-based action understanding is detached, disengaged, i.e. purely spectatorial in nature (De Jaegher & Di Paolo 2007). Quite the opposite: what the mirror mechanism really suggests is that one may make sense of other people by means of her own motor cognition even when she is just witnessing their actions. In other words, what it really suggests is that even witnessing other people's actions can be considered as a limit case of an actual interaction (Sinigaglia 2010).

Grasping with the eyes

To what extent is one's own motor cognition reused when witnessing someone else's action? And how does such motor cognition reuse impact on the witness's behaviour?

Both questions can be answered by assessing how people gaze at both their own and another's action.

Target-specific proactive gaze shifts are crucial for planning and executing object-related hand actions (Bowman et al. 2009; Brouwer et al. 2009; Johansson et al. 2001; Land et al. 1999). Strikingly, people witnessing rather than performing object-related hand actions also make proactive eye movements. The witness's gaze typically grabs the target well before the actor's hand, being their time relation similar to that exhibited by the actor's own gaze and hand (Flanagan & Johansson 2003; Falck-Ytter et al. 2006; Rotman et al. 2006; Webb et al. 2010). Such similarity becomes highest when people are able to take advantage of specific motor cues in selecting the target of another's action (Flanagan & Johansson 2003; Falck-Ytter et al. 2006). In particular, people are faster in grasping the target object of witnessed hand actions when they can capitalize on a pre-shaping hand with a specific grip with respect to when they cannot even when the target is not previously known (Ambrosini et al. 2011a).

This suggested that the same motor cognition may drive people's eye movements while executing and witnessing those actions (Flanagan & Johansson 2003; Falk-Ytter et al. 2006). As highlighted by the mirror mechanism research, witnessing someone else's action recruits the same premotor and parietal motor resources as if the witness were performing those actions herself. Such motor recruitment would allow the witness not only to understand what another invidual is doing, but also to implement specific eye motor programs, thus grabbing the target of action ahead the actor's hand, even when it is not previously known.

In a repetitive transcranial magnetic stimulation study Marcello Costantini, Ettore Ambrosini, Pasquale Cardellicchio and I have very recently demonstrated that the mirror-based motor cognition reuse may actually play a causal role in driving people's gaze (Costantini et al. forthcoming). Indeed, virtual lesion of the left ventral premotor cortex not only selectively impaired gaze proactivity while viewing grasping actions, but the impairment was so marked that the proactivity exhibited while witnessing grasping hand actions became the same as that recorded while witnessing mere touching actions, that is actions that are devoid of any motor cues, such as that provided by a pre-shaping hand, which one would employ to identify their target action in advance with respect to the actor's making contact with it. These effects were absent after the virtual lesion of the left frontal eye fields and of the posterior part of left the superior temporal sulcus, respectively.

So far so good. But what happens if people are not really able to perform the witnessed action? Several studies demonstrated that the mirror-like motor recruitments are strictly correlated to one's own motor cognition. Viewing videos of classical ballet or capoeira has been shown to activate differently the pre-motor cortex of participants, depending on whether they were experts in classical ballet or in capoeira

(Calvo Merino et al. 2005, 2006; see also Cross et al. 2006). Similar results have been obtained in a series of experiments on other skilled actions such as piano (Haslinger et al. 2006) or basketball playing (Aglioti et al. 2008).

These studies, however, just focused on what philosophers call "general abilities" as distinct from "specific abilities" (Mele 2003). The general abilities of an individual characterize her motor cognition irrespectively of temporary obstacles to acting. By contrast, specific abilities refer to what an individual is in a position to do at a particular time. Thus a natural question arises as to whether and to what extent motor cognition reuse can be affected not only by what people can do but also by what they are actually in position to do.

Both general and specific abilities to perform a given action have been demonstrated to affect success on tasks involving imagination. Upper limb amputees are impaired in tasks requiring mental hand rotation (Nico et al. 2004), and temporarily preventing people from accomplishing a given hand action also impairs their performance (Sirigu & Duhamel 2001; Shenton et al. 2004; Ionta et al. 2007; Ionta & Blanke 2009). Even the hand posture adopted by participants can modulate the motor facilitation effect of the motor imagery (Vargas et al. 2004; Fourkas et al. 2006; Mercier et al. 2008). Might specific abilities to act similarly affect witnessing (rather than imagining) an action such as a grasping action?

Ettore Ambrosini, Marcello Costantini and I have tackled this issue, by recording eye movements while participants witnessed either grasping or mere touching actions with their hands in one of two different positions (Ambrosini et al. 2011b). In one condition, their hands were unconstrained; in the other condition, their hands were tied behind their backs so that they were temporarily unable to perform the action observed. If the motor cognition reused when witnessing someone else's action really closely resembles that which would be used in performing an action of the same type (as the mirror mechanism research suggests), we expected body posture to affect people target detection as measured by the proactive nature of their gaze behaviour. No such effect of body posture would be expected if motor cognition were not so deeply involved in action observation.

The results showed that when participants' hands were unconstrained, the proactivity of their gaze behaviour was significantly higher while observing a grasping action than when they observed a mere touching hand. However, their gaze behaviour was dramatically impaired when participants observed others' actions while their own hands were tied behind their back.

All of this was not only consistent with the mirror mechanism research, but also shed new light on how deeply motor cognition might be reused while witnessing someone else's action. When the witnessed action did not fit with the specific abilities of the witness, her motor cognition was prevented from successfully and proactively driving her saccadic movements. On the contrary, being in the position to perform the

observed actions enabled the witness to fully recruit the corresponding motor cognition, thus proactively gazing at the target of others' behaviour.

Finally, one could wonder what would happen if the actor (rather than the witness) were not in the position to successfully perform her action. For instance, what would happen if the actor were not able to actually grasp the intended object, being the latter just out of her reach? Would this impact on the witness's eye behaviour? Would the witness's motor cognition be critically involved even here?

Object reachability has been found to affect people's reuse of suitable motor cognition when dealing with action-related objectual features. Indeed, the power of an object such as a handled mug to afford a suitable grip (e.g. a precision grip) has been shown to depend on the object's falling within the actor's reaching space (Costantini et al. 2010). Interestingly, this holds not only when people are performing a grasping action but also when seeing an affording object without any intention to act upon it (Cardellicchio et al. 2011). Might people's reuse of their motor cognition be also affected by the possibility for another actor to actually reach an object?

In a further study, we recorded eye movements while participants viewed an actor either grasping or touching objects (Costantini et al. submitted). In all the conditions the target objects were located either within or just outside actor's reach. The rationale was similar to that of the previous experiments. If people really reuse the same motor cognition both when executing and witnessing a given action such a grasping action, then one should expect that the actor's reachability might affect the witness's gaze behaviour, being their eye movements slower in latching onto the target, when the object is not actually reachable for the actor than when it is.

The results showed that this was actually the case. Indeed, participants were more accurate and faster in gazing at the targets while witnessing a grasping action than while witnessing a mere touching hand. However, the accuracy and proactivity of their eye movements were significantly impaired when the targets of grasping actions were just out of the actor's reach. This suggests that a relevant motor cue such as a pre-shaping hand is not enough per se to prompt proactive eye movements. Gaze proactivity is also dependent on the actor's being in the position to actually reach her intended target. If people do capitalize on their own motor cognition while looking at the target of others' actions, than the proactivity of their eye movements may depend on the spatial relations constraining the exploitation of their motor cognition.

The space of action

Let me have a closer look at the spatial constraints on motor cognition. When people are performing an action such as grasping a given object, the use of their motor cognition is spatially constrained (Jeannerod et al. 1995), depending on the actual extent of their own reaching space. As it is well-known, the reaching space evolved primarily to subserve action (Rizzolatti et al. 1997): not only is it motor in nature but also its range varies in size according to one's own reaching abilities (Sinigaglia & Brozzo 2011). Indeed, there is plenty of evidence in monkeys (Iriki, Tanaka, & Iwamura 1996) as well as in healthy (Maravita et al. 2002; Serino et al. 2007) and brain damaged (Farnè et al. 2005; Farnè et al. 2007; Neppi-Mòdona et al. 2007) humans that the extent of the reaching space can be modified by active tool use. In particular, line-bisection studies on patients with selective neglect for peripersonal space showed that tool use might reduce or increase the severity of the neglect (Neppi-Mòdona et al. 2007). Likewise, tool use in patients with visuo-tactile extinction has been demonstrated to modulate the severity of their extinction (Farnè et al. 2005; Farnè et al. 2007).

What the findings mentioned in the previous section strongly suggest is that the reaching space may also constrain the motor cognition use when people are either seeing a given object or witnessing someone else's action rather then acting or meaning to act themselves. Now the question is whether the spatial constraint on the motor cognition might also be affected by tool use as well as whether not only actively using a tool but also witnessing someone else using a tool might succeed in this.

In a series of behavioural experiments carried out by Marcello Costantini, Ettore Ambrosini, Vittorio Gallese and I, we took advantage of the spatial alignment effect referring to a decrease of reaction times when people execute an action congruent with that afforded by a seen object (Bub & Masson 2010), in order to assess whether and to what extent both using a tool and witnessing someone else doing it impact on one's own reaching space (Costantini et al. 2011). Previous evidence showed that this effect is spatially constrained, occurring only when the seen object is actually ready to hand (Costantini et al. 2010).

Participants were instructed to replicate a reach-to-grasp movement as soon as a task irrelevant go-signal (e.g. a mug located either within or outside the reachable space of participants with the handle orientation either congruent or incongruent with the grasping hand) was presented. The experimental task was performed before and after a training session in which the participants were requested to actively use, or passively hold, a grasping tool such as a garbage clamp, as well as to observe someone else using the garbage clamp while holding or not holding the same tool or holding a tool that was similar in terms of goal (e.g. a pair of pliers) or length (e.g. a rod).

The results showed that both performing and witnessing tool-action might affect motor cognition reuse, by extending one's own reaching space. Indeed, not only using a grasping tool such as a garbage clamp but also witnessing someone else using that tool made participants sensitive to the congruent affording feature of the viewed object (the oriented handled mug) even when the latter was presented out their reach. Tool action impacted on participants' own reaching space in either case. Strikingly, this effect was absent both when the participants merely held the tool and also when they witnessed someone else's tool action holding a tool that was incompatible with the witnessed action with respect to either its goal or its range.

While the first finding is fully consistent with previous tool-use research (Sinigaglia & Brozzo 2011), the second one is in line with what we found in the eye movement study demonstrating that one's motor cognition may proactively drive her own gaze just when she is in the position to perform the witnessed action. Indeed, witnessing another's tool action might impact on one's own reaching space only provided that she shares with the witnessed actor the possibility to act, by holding a tool compatible with the goal and with the spatial range of her action. When these conditions are met, the witnessed tool action can be mapped by the mirror mechanism onto the witness's motor cognition, and this is not without consequences for her reaching space. Thus, actually being in the position to act turns out to be crucial for the mirror-based reuse of one's own motor cognition not only when people have to guess someone else's action-target but also when they have to witness the actor reaching it by means of a tool.

The spatial constraint of mirror-based motor cognition reuse, however, goes even deeper than this. When it comes to acting upon objects or to perceiving their affording features the existence of a spatial constraint may not come as a real surprise. Perhaps, it may come as a surprise that the range of this spatial constraint can be affected by witnessing someone else's action. But what if it is the case that just the possibility for another individual to act upon an object might impact on the spatial constraint of one's own motor cognition?

To tackle this issue, we again took advantage of the spatial alignment effect (Costantini et al. 2011). Participants were instructed to replicate a reach-to-grasp motor act, with either their right or their left hand, on the presentation of a task-irrelevant go signal depicting a 3D scene with a mug placed on a table, with its handle oriented towards the right or the left (i.e. congruent or not with the movements to be executed). The mug could be located either within or outside the reaching space of the participants. In half of the trials, however, a virtual actor such as an avatar was seated at the table. The results not only corroborated our previous findings (Costantini et al. 2010), showing that the spatial alignment effect occurs when the congruent mug falls within the reaching space of the participants, but extended them, demonstrating that the spatial alignment effect occurs even when the mug was presented outside the reaching space of the participants but within the reaching space of the avatar, being congruent with both the avatar's and the participants' grip.

A TMS study recently provided these behavioural findings with a neuronal counterpart (Cardellicchio et al. 2011). The left primary motor cortex was magnetically stimulated and the motor evoked potentials (MEPs) were recorded from the right first dorsal interosseus and opponens pollicis while participants viewed 3D stimuli depicting a room where a virtual individual such as an avatar was seated on a table

with a handled mug ready to her hand. The mug could be located either within or outside the reaching space of the participants. Higher MEPs were found both when the mug was near enough to be actually reachable for the participants and also when it was out of reach for them provided that it was ready to the avatar's hand. This means that the mere sight of an affording object located outside the reaching space of the participants but within the reaching space of a virtual individual such as an avatar might evoke a suitable motor act similar to that afforded by an object falling within the participants' reaching space.

How to account for the fact that the use of one's own motor cognition can be affected by the presence of a potential rather than an actual actor? And how to account for one's sensitivity to someone else's being afforded by the surrounding world? The proposal is that all of this can be explained by means of an interpersonal bodily space representation allowing one to map the body of other people in terms of their actual motor possibilities (Costantini & Sinigaglia 2011).

There is evidence for the existence of an interpersonal bodily space mapping in the visuo-tactile domain (Sirigu et al. 1991; Reed et al. 1995; Maravita et al. 2002; Thomas et al. 2006; Ishida et al. 2009). In particular, this spatial mapping has been shown to play a crucial role in processing sensory events on others' body at the behavioural level (Thomas et al. 2006). Similar results have also been found at the neuronal level. Visuo-tactile neurons have been recorded from the ventral intraparietal area (VIP) of the macaque brain (Ishida et al. 2009). A signification portion of these neurons exhibited both visuo-tactile RFs on the monkey's body and visual RFs close to the experimenter's body, selectively responding to a visual stimulus delivered both within the peripersonal space of the monkey and also at 120 cm from the monkey's body but close to the experimenter's one.

Our findings extend the interpersonal bodily space representation to the motor domain, highlighting that such representation enables one not only to map the sensory stimuli around the body of others, but also to grasp their body as a situated body which might be afforded by the surrounding things, provided that the latter are ready to hand. This explains why one may reuse her own motor cognition when witnessing someone else either actually acting or being in position to act. The motor nature of the interpersonal bodily space representation seems also to bridge the gap between the motor cognition reuse involved in representing action-related objectual features and that subserving another's action processing, playing a key role in understanding from the inside what another individual can really do (Costantini & Sinigaglia 2011). Indeed, by mapping another's reaching space, this representation provides one with what is really ready to another's hand, thus making the action-related features of the surrounding things useful for grabbing her effective action possibilities. And, as our eye experiments showed (Costantini et al. 2011), this is not without consequences for the onlooker's behaviour itself. Just like in the case of seeing a graspable object ready

to a virtual individual such as an avatar, witnessing someone else actually launching her hand towards one of two objects in order to grasp it may recruit the suitable motor cognition only provided that the target of the witnessed action is mapped onto the reaching space of the agent. When objects are mapped close enough to an agent to be reached, they are automatically represented as potential targets for her actions; the onlooker's motor cognition can therefore be immediately applied to them, thus proactively driving her gaze. On the contrary, when objects are mapped out of the agent's reach, they are not automatically represented as potential targets of her actions; accordingly, the onlooker's motor cognition cannot be immediately related to them, and this impact on the proactivity of her gaze behaviour.

Concluding remarks

To sum up, taken together the above mentioned studies clearly indicate that mirror-like motor cognition reuse is selectively modulated by either the agent's or the witness's being actually in the position to act, being such modulation especially related to the witness's personal and interpersonal bodily space representation. Indeed, the recruitment of one's motor resources while witnessing someone else's action is strongly affected by her own actual possibility to act as well as by the agent's actual possibility to successfully achieve the intended outcome. In addition, this is true not only when witnessing someone else acting but also when witnessing another individual being about to act, as the avatar experiments point out. This is likely to be due to an interpersonal bodily space representation allowing one to map the body of other people in terms of their actual motor possibilities. It is this mapping that provides the witness with an immediate understanding of what the agent is actually in the position to do, thus allowing the former to represent the latter in terms of her own motor potentialities. Although this point needs to be further investigated, it does follow that variations in the witness's bodily space representation should impact on her mapping of others' action space, thus modulating the understanding of their actions.

Elsewhere, I have argued that one makes primarily experience of her own body "as 'source' or 'power' for action, i.e. as the variety of motor potentialities" defining the horizon of the surrounding world in which she lives (Gallese & Sinigaglia 2010, p. 746). The above-mentioned findings suggest that not only one's own body but also the body of other people is primarily experienced as a situated body – as a body embedded in its own space which encompasses all the affording features, that is, all the motor potentialities that are effectively ready-to-hand.