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CICLO XXII

OLFACTION IN ACTION

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1. General introduction

1.1 MULTISENSORY ASPECTS OF ACTIONS

One of the classic roles attributed to multisensory integration is that of producing a unitary percept of objects (Newell, 2004). We can recognize a spoon not only by looking at it but also by touching it when it is out of view. We can recognize a species of bird by seeing it, by using visual information about its size, shape, and colours, and also by hearing its song. However, different sensory modalities are used in concert not only to perceive objects but also to represent actions (Fogassi & Gallese, 2004). In this respect, a first fundamental role of multisensory integration is to help us to plan and execute actions. Indeed, in our daily life most of the actions we perform rely on sensory information, and in order to act appropriately, we often have to process in parallel information arriving via more than one sensory modality. The act of kicking a ball, for example, requires the integration of visual, proprioceptive, and tactile modalities. Writing is another example of an action that, to be accomplished accurately, requires the integration of visual, proprioceptive, and tactile information. In addition, recognizing and understanding what other individuals are doing depends on multimodal information (Fogassi & Gallese, 2004). As an example, even without seeing a person pouring water into a glass, we can recognize this action from the sound made by the flowing liquid. Thus, the retrieval in our brain of the representation of a given object, individual, or action greatly benefits from information arriving through different and multiple sensory modalities.

To date, crossmodal links between vision, audition, sense of touch, and proprioception have been extensively documented for one of the most common actions we experience: grasping an object by using hands (Johansson & Westling, 1984; Klatzky & Lederman, 1987; Klatsky, Lederman, & Reed, 1987; Goodwin, Jenmalm, & Johansson, 1998; Jenmalm, Dahlstedt, & Johansson, 2000; Klatzky, Pai, & Krotkov, 2000; Van Beers, Baraduc, & Wolpert, 2002; Patchay, Castiello, & Haggard, 2003; Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Gazzola, Aziz-Zadeh, & Keysers, 2006; Patchay, Haggard, & Castiello, 2006; Zahariev & MacKenzie, 2007; Castiello, Tubaldi, Ansuini, Giordano, & Grassi, 2007; Etzel, Gazzola, & Keysers, 2008). In particular, the contribution of multimodal information has been shown both when an individual controls own hands grasping an object (Van Beers et al., 2002; Patchay et al., 2003; Patchay et al., 2006; Zahariev & MacKenzie, 2007) and when tires to understand the grasping action performed by somebody's hands (Aziz-Zadeh et al., 2004; Gazzola et al., 2006; Etzel et al., 2008).

1.1.2 Execution of hand grasping actions

During the execution of hand grasping actions, we transport our hand near the to-be-grasped object and we attuned gradually the hand to the object's features. But how information coming from our senses guides these actions?

1.1.2.1 The role of visual information

To investigate the role of visual information when grasping, a number of behavioural studies has specifically investigated hand kinematics (Jackson, Jackson, & Rosicky, 1995; Tipper, Howard & Jackson, 1997; Tipper, Howard, & Houghton, 1998; Castiello, 1996; Castiello, 1998; Castiello, 1999; Kritikos, Bennett, Dunai, & Castiello, 2000; Kritikos, Dunai, & Castiello, 2001). These studies asked participants to reach-and-grasp a visual target presented either in isolation or in conjunction with a visual non-target object (distractor) of a different size than the target. In general, it was found a progressive opening of the hand, with straightening of the fingers up to the pick aperture, followed by a gradual closure until the target was grasped. Furthermore, the maximum hand aperture increased with the size of the visual target-object, i.e., it was bigger for the large than for the small target. Most importantly, when performing a reach-to-grasp movement towards a large target in the presence of a smaller distractor, maximum hand aperture (i.e., the maximum distance reached by the index finger and the thumb during reaching) was smaller than when the same target-object was grasped in the absence of a distractor. Conversely, when the target was small and the distractor was large, maximum hand aperture was larger than when the same target was presented in the absence of a distractor.

Altogether these findings suggest that merely seeing an object activates the action plans associated with it (e.g., hand shaping). This was taken as an evidence for a visuomotor mechanism which converts quickly and effortlessly objects' geometry into an appropriate 'grasp' motor plan (Castiello, 1996; Castiello, 1998; Castiello, 1999; Kritikos et al., 2000; Kritikos et al., 2001). This mechanism (or transformation) would be at the basis for the visual guidance of hand grasping actions, enabling the unfolding of a hand shaping which is matched to objects' structure.

1.1.2.2 The role of tactile information

The first attempt to investigate the multimodal nature of the visuomotor mechanism underlying grasping has been conducted by Gentilucci, Daprati, & Gangitano (1998). In their experiments, participants reached and grasped a visual target-object presented in different sizes (small, medium, and large target) with one hand, while holding another, an unseen distractor of different sizes (1-cm either smaller or greater than the target) in the other hand. The main finding was that the size of the distractor did affect the kinematics of the grasping executed with the other hand. In particular, maximal hand aperture decreased and increased when the distracor was smaller and larger than the visual target-object, respectively. However, the effect of tactile information was only observed when the visual target-object was small and manipulation was performed using the right hand. This rendered unclear what caused the effect.

In a series of subsequent investigations Patchay et al. (2003; 2005) confirmed and extended these results. By using a similar experimental paradigm, these authors found that maximum hand aperture for the visual target was proportional to the dimension of the distractor which was manipulated proprioceptively with the other hand. Furthermore, analogous patterns were observed when the distractor was manipulated with either the left or the right hand. Noticeably, the effect of tactile information occurred only when the distractor was actively grasped. The effect was absent when the non-reaching hand received passive tactile and proprioceptive stimulation.

Overall these findings show that exploring a large and a small object activates the movement parameterization which corresponds to the size of that object, i.e., big and small hand aperture, respectively. This signifies that selection of the appropriate 'grasp' motor plan for interacting with an objet can be based on tactile cues. Therefore, the mechanism underlying the guidance of actions is not only sensitive to the information conveyed via vision but also via the sense of touch.

1.1.2.3 The role of auditory information

When using hands to manipulate objects and interact with surfaces we generate contact sounds. These auditory events provide important information concerned with the interaction between the moving effectors and the acted upon object. In particular, the contact sound signals both functional consequences and completion of manipulative actions. For instance, the 'crash' sound associated with our hands breaking a walnut can be considered as a contact sound. Upon hearing the 'crash', we become aware of having broken the shell, thus, we stop the walnut handling, and we bring the husk to our mouth.

Zahariev & MacKenzie (2007) have recently focused on the role played by contact sounds for the planning and the execution of hand grasping actions. In their experiments, participants reached towards and grasped a visual target (i.e., a wooden cube) either in the absence or in the presence of a 'virtual' contact sound. The contact sound was delivered in the end of the reaching movement, when digits closed around the visual target-object. Their main finding was that reach duration was shorter for the contact sound compared to the no contact sound condition. This result was taken as an evidence of the effect that auditory information might exert on the organization of hand grasping movements. However, the specific reason of why the presence of a contact sound reduced reach duration leaving unchanged hand kinematics was unclear. Furthermore, the delivered contact sound corresponded to the sound of a cork popping out of bottle, a sound which is not normally generated when touching a wooden block. Therefore, the nature of the effect caused by the contact sound remained unexplained.

A subsequent investigation addressed this issue by adopting a similar procedure (Castiello et al., 2007). Here the sound produced by digits which made contact with objects covered with different materials (i.e., aluminium, paper, string, wool) was recorded. In a first experiment, either one of the recorded contact sounds or a synthetic sound was administered to participants. The task was to reach towards and grasp a visual target-object. The foremost result was that the contact sound did affect movement kinematics. Specifically, both reach duration and the time of hand closure around the visual target decreased when the administered contact sound corresponded to the sound which was actually generated by the forthcoming contact with that visual target. Whereas, when the administered contact sound differed from that associated with the interaction between the hand the visual targe, both reach duration and the time of hand closure around the target increased. Therefore, hearing sounds which will be generated during the end part of action, when the hand touches the visual target-object, facilitates the 'grasp' motor plan selected for that specific target.

Further support to this proposal comes from a second experiment (Castiello et al., 2007). Participants were requested to reach towards and grasp a visual target which had the upper and the lower part covered with different materials (e.g., wool and paper, respectively). This task was performed in the presence of a contact sound associated with the material covering one of the two parts of the visual target (e.g., 'touching-wool' sound or 'touching-paper' sound). Noticeably, when the presented contact sound was 'touching-wool' and 'touching-paper', the probability that participants grasped the visual-target object by the wool surface and the paper surface increased above chance, respectively.

Altogether, these findings demonstrate that selection of the 'grasp' motor plan for interact with an objet can be based on contact sounds. This evidence extends the sensitiveness of the mechanism underlying the guidance of actions to the auditory information.

1.1.3 Understanding hand grasping actions

As well as we grasp objects in order to manipulate them or to use them as to act upon other objects, we are often confronted with the task of understanding grasping actions performed by others. How information coming from our senses enables the full comprehension of these actions?

1.1.3.1 The role of visual information

A vast amount of studies using positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) has investigated how different visual features of others' actions affect an observer's cerebral activity (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Hari et al., 1998; Avikainen, Forss, & Hari, 2002; Buccino et al., 2004; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Gazzola & Keysers, 2009; Turella, Erb, Grodd, & Castiello, 2009; Peeters et al., 2009). These studies asked participants to watch video-clips representing either a hand acting upon an object or a control condition (i.e., solely a hand, solely an object, or a hand resting alongside an object) while functional imaging scanning was performed. Then, cerebral activation elicited by viewing the actions of other individuals was compared to cerebral activity elicited by the control condition.

In general, the premotor cortex, the primary motor and somatosensory cortices, several parietal areas, and the posterior temporal-occipital cortex were consistently activated for action observation. Most importantly, this sensorymotor circuitry, termed as the action observation system (AOS), was sensitive to different visual features of the perceived action (Buccino et al., 2001; Hamilton & Grafton, 2006; Hamilton & Grafton, 2008; Majdandžić, Bekkering, van Schie, & Toni, 2009). Specifically, Buccino et al. (2001) found that observation of a series of actions performed upon an object with the mouth, the hand and the foot, respectively, led to the activation of different loci within the premotor and the parietal cortex, depending on the effector involved. Therefore, the visual representation of different effectors appears to be segregated within the AOS. Furthermore, the level of AOS activity depended on the nature of the moving effector (human *vs.* robotic arm-hand ensemble) (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). Therefore, visual information regarding the type of agent is also represented within the AOS.

By using a repetition suppression (RS) paradigm, recent fMRI investigations have confirmed and extended the notion that the AOS represents visual items of others' actions. In this respect, Hamilton & Grafton (2006) showed that repetitive observation of a hand grasping a visual target-object (e.g., a cookie) results in a reduction of the fMRI signal recorded from the intraparietal areas. Noticeably, the intensity of this signal returned to normal level when the same action, but performed upon a new visual target (e.g., a disk), was presented. This dishabituation indicates that the AOS codes the visual aspect of the target-object. A similar decrease in fMRI signal was also recorded from the inferior parietal cortex when repeatedly observing a hand movement aimed at opening a box (Hamilton & Grafton, 2008). Only the presentation of the same movement but aimed at closing the box restored the original intensity of the signal. Thus, the AOS also represents visual physical consequences of an action. In this vein, Majdandžic et al. (2009) showed that fMRI signal elicited by observation of a complex action (i.e., reach towards, grasp, and place an object) decreased within the dorsal premotor cortex following the repetitive view of the ‘place’ component (i.e., placing the object on the upper yellow slot). When the ‘place’ component changed (i.e., placing the object on the lower blue slot), original intensity of fMRI signal was recovered. Therefore, the AOS represents visual end-states of others’ actions.

Altogether, the present findings demonstrate that the AOS is sensitive to different visual features of other’s actions. This would allow to achieve an internal description of actions which, in turn, would enable action understating.

1.1.3.2 The role of auditory information

The interaction between hands of somebody acting upon an object or a surface very often produces contact sounds. For instance, everyone has experienced the sound of somebody’s hands ripping a paper sheet. By merely hearing this sound, we understand which effectors the other individual moves (e.g., hands rather than mouth), which type of object is manipulated (e.g., paper rather than iron), how and to which purpose the object is handled (e.g., ripping rather than folding in half). The demonstration that the human AOS is engaged when a person hears the contact sound generated by other’s action comes from two recent investigations. In first instance, Gazzola et al. (2006) conducted an fMRI experiment in which participants were presented with sounds of either bimanual hand actions or mouth actions. As auditory control stimulation, either environmental sounds or phase-scrambled versions of the action sounds were administered. The authors found an increase in activation within both the premotor and the inferior parietal cortex when participants listened to actions with respect to control auditory stimulation. Noticeably, the dorsal part of the premotor cortex responded more to sounds generated by hand actions than mouth actions. Whereas, the opposite pattern was found for the premotor ventral cortex. Therefore, the AOS is not only sensitive to auditory features of the other's actions but, importantly, the action-related auditory information is segregated depending on the type of moving effectors.

A subsequent fMRI investigation confirmed and added to the contribution of audition to other's action representation (Etzel et al., 2008). Specifically, a computational classifier was exposed to premotor activity evoked by the perception of sounds related to hand and mouth actions. By means of this training, the classifier learned to distinguish whether a participant had heard a hand or a mouth action. Noticeably, by using this auditory experience, the classifier was also able to recognize whether brain activity detected within the premotor cortex of the participant was associated with the execution of hand and mouth actions. This result indicates that while listening other's actions, the pattern of activity within the AOS is a significant source of information regarding the nature of these actions.

Altogether, the present findings demonstrate that auditory features of others' action are represented within the AOS and contribute to an internal description of the action. Thus, audition plays a central role in action understanding.

1.2 THE PRESENT RESEARCH

An extensive body of evidence stemming from investigations on hand grasping actions has provided support for the existence of robust crossmodal links in both action performance and understanding (Van Beers et al., 2002; Patchay et al., 2003; Aziz-Zadeh et al., 2004; Gazzola et al., 2006; Patchay et al., 2006; Zahariev & MacKenzie, 2007; Etzel et al., 2008). The multisensory integration of inputs coming from vision, audition, the sense of touch, and somatosensation appears to be the norm rather than an exception within the action domain. People typically integrate the multiple streams of sensory information coming from each of their senses in order to both perform own actions and generate other's action representations. Yet no studies, to date, have examined if this extends to information conveyed via olfaction.

In order to shed light on the role played by olfaction in action performance, I applied kinematic techniques to investigate the effects that olfactory stimuli might have on a complex motor system such as that subtending hand grasping actions. I first investigated whether and how the presence of an odour associated with a distractor does affect hand kinematics when reaching towards and grasping a visual target (Chapters 3 and 4). Specifically, in the experiments described in Chapters 3 and 4, I tested whether graspable objects' odours do affect both the hand kinematics and the temporal parameterization of the arm which transports the hand towards the visual target. Continuing on this analysis, I tested whether prior knowledge regarding the visual target may reduce the contribution of olfactory information to the selection of ‘grasp’ motor plans (Chapter 5). To this end, I considered both temporal and kinematical parameterisation of hand grasping movements. Finally, I tackled the issue regarding gender differences in olfactory information processing within the action domain (Chapter 6). In this respect, I assessed whether the participants’ gender modulates the effect that olfactory information has on the temporal parameterisation of arm movement. This investigation would allow to demonstrate that the ability to use olfactory information for the control of action varies between males and females.

With respect to the role played by olfaction in action understanding, I adopted the fMRI technique to address the possibility that an individual uses olfactory information to understand other’s people actions (Chapter 7). I targeted activity triggered by perception of different hand grasping actions within the AOS. In particular I tested whether activity elicited by somebody’s hands grasping a target-object signalled via olfaction (i.e., an olfactory target) differs from the activity elicited by an identical, but mimed action (i.e., a hand grasping movement performed without the presence of an object). This investigation would allow to document the ability of the human AOS to discriminate two actions on the basis of olfactory information. Furthermore, I assessed whether the specification of the target for another person’s action via both vision and olfaction elicits subadditive activity within the AOS. This would allow to document the ability of the AOS to integrate action-related visual and olfactory information.

The results stemming from the kinematic studies and the fMRI investigation have been discussed in light of current theories proposed to explain how the CNS controls own actions and represent other's actions in a multisensory fashion (see 'Discussion' sections for each experimental chapter and Chapter 8).

2. General methods

In this chapter the methods and the procedures which are common to all the experiments included in the present thesis will be described. Exceptions will be reported within each experimental chapter.

2.1 PARTICIPANTS' CHARACTERISTICS

All the participants who took part in the present series of experiments showed right-handed dominance and reported normal olfaction, no history of olfactory dysfunction, and normal or corrected-to-normal vision. They were naïve as to the purpose of the experiments and gave informed consent to participate in the study. The experimental procedures were approved by the Institutional Review Board at the University of Padova and were in accordance with the declaration of Helsinki.

2.2 KINEMATIC EXPERIMENTS

2.2.1 General Procedures

In all the experiments, participants sat on a height-adjustable chair in front of a rectangular table with the elbow and wrist resting on the table, the forearm horizontal, and the arm oriented in the parasagittal plane passing through the shoulder (see Figure 2.2.1.1a).

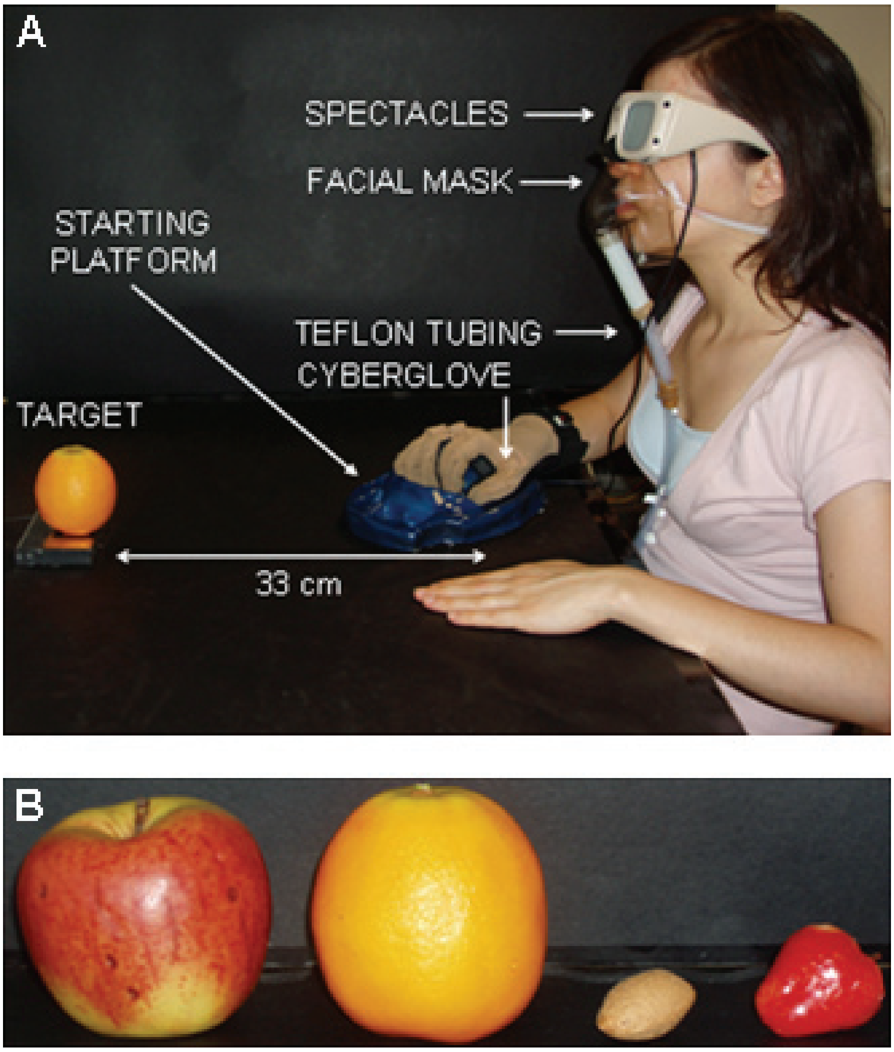

Figure 2.2.1.1 The experimental set up and the visual targets. (A) Labels indicate the parts composing the experimental set up. (B) The visual targets defined as 'large' were an apple and an orange, whereas those defined as 'small' were an almond and a strawberry. Note that the starting platform was designed with slight convexities dictating a natural flexed posture of the fingers as to make sure that the initial posture of hand was similar for all participants across trials.

At the beginning of each experimental trial, participants placed their right hand on a starting platform which was located slightly to the left of theirs right shoulder (see Figure 2.2.1.1a). Participants' vision was controlled using spectacles fitted with liquid crystal lenses (Translucent Technologies Inc., Toronto, Ontario, Canada) (see Figure 2.2.1.1a). When participants placed their right hand on the starting platform, crystal lenses changed from clear to opaque preventing participants' vision. Then, the experimenter placed a target-object on the working surface. The target was aligned with the participant's body midline and located at 33-cm-distance from the hand starting position (see Figure 2.2.1.1a). An auditory tone (850-ms duration, 65-dB sound pressure, and 800-Hz frequency) indicated the onset of odour delivery. Following 3 s, a similar tone indicated the offset of odour delivery. In general the sequence of events proceeds as follows: (*i*) after a time interval of 500 ms, the tone was presented again; (*ii*) upon hearing the tone, participants were instructed to reach towards, grasp and lift the visual target-object; (*iii*) when the hand was lift from the starting platform, crystal lenses changed form opaque to clear rendering the target visually available. Please note that for the experiment described in Chapter 5, the sequence of events was slightly different. For the sake of clarity such exception is reported within the 'Methods' section for this chapter.

For all the experiments (see Chapters 3, 4, 5, and 6) participants were instructed to reach and grasp at a natural speed the visual target by opposing the thumb to the four fingers and not to grasp the target-object by the stem. The experimenter visually verified that participants complied with all task requirements during each trial. Trials which did not meet set criteria were discarded and repeated. Sufficient time (10 s) was allowed between trials to recover from any odour adaptation (Hummel, Knecht, & Kobal, 1996).

2.2.2 Stimuli and apparatus

The visual targets consisted of one of four different plastic fruits grouped on the basis of their natural size: an orange and an apple were considered as the large objects, whereas, a strawberry and an almond were considered as the small objects (see Figure 2.2.1.1b). Plastic fruits were used in order to maintain consistent visual attributes and sizes similar throughout the period of experimentation. The odour stimuli corresponded to the stimuli described above. Odour solutions of strawberry, almond, orange, and apple were obtained mixing 6000 ml of prophylenic glycol and 180 ml (3%), 60 ml (1%), 420 ml (7%), and 45 ml (0.75%) of the specific odorant compound, respectively (Cerizza, Milan, Italy). A custom-built computer-controlled olfactometer (Department of Experimental Psychology, University of Oxford) was used to deliver the odour stimuli. The olfactometer was capable of rapid delivery of discrete odour pulses in the absence of tactile, thermal, or auditory variation. Each odour generator consisted of a glass boat containing one of four odour solutions. A fifth glass boat containing prophylenic glycol was used for the delivery of odourless air. The air passed over the odour solutions and the prophylenic glycol at a flow rate of 8 l/min and it was delivered on both nostrils to subjects via Teflon tubing to a facial mask (see Figure 2.2.1.1a).

2.2.3 Recording techniques

At the beginning of each experimental session, participants were requested to wear in their right hand a glove (CyberGlove, Virtual Technologies, Palo Alto, CA) (see Figure 2.2.1.1a and Figure 2.2.3.1).

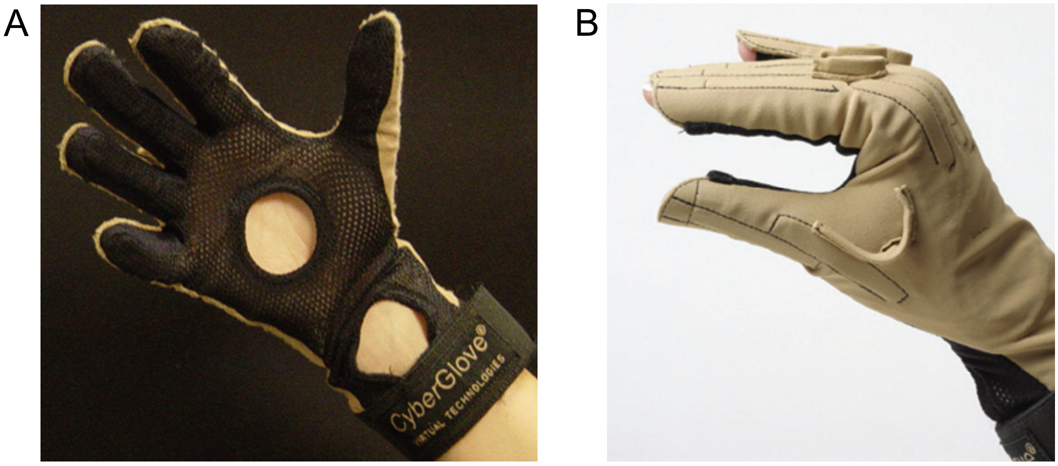

Figure 2.2.3.1 Bottom and side views of the Cyberglove worn by each participant (Panel A and B, respectively).

The resistive sensors embedded in the glove are extremely thin and flexible being virtually undetectable and allow the recording of hand posture. In particular, it is possible to record the angular excursion at the level of both metacarpal-phalangeal (*mcp*) and proximal interphalangeal (*pip*) joints of the thumb, index, middle, ring, and little fingers (see Figure 2.2.3.2). Furthermore, the sensors placed between the digits allow for recording the angular distance for each pair of adjacent digits (i.e., thumb-index, index-middle, middle-ring, and ring-little) (see Figure 2.2.3.2).

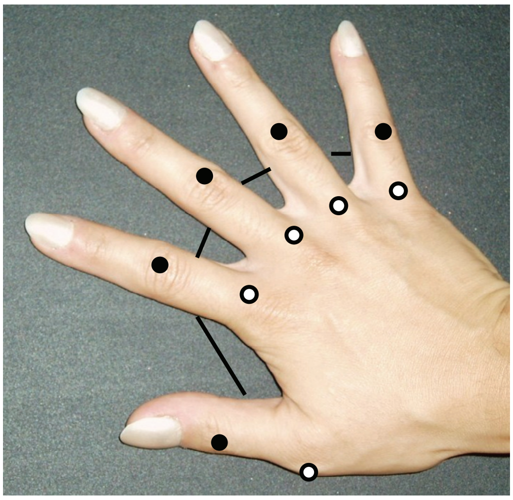

Figure 2.2.3.2 A schematic view of metacarpal phalangeal (white dots) and proximal inter phalangeal joints (black dots), and distances between adjacent digits (black segments) from which angular excursion and adduction-abduction angles can be recorded by means of the CyberGlove.

In order to obtain a reference hand posture, once the glove was worn, participants were requested to place their right hand flat on the table with the digits straightened, close to each other and to hold that position until baseline angular values for all digits' joints and distances were recorded. Baseline angular values for all digits' joints and distances were defined 0 degrees when all digits' joints and distances were maintained straight and together in the plane of the palm, respectively ('reference hand posture'). Digits' flexion was assigned positive values whereas digits' extension was given negative values with respect to the baseline. Digits' angular distance was reported on a continuum of negative values with respect to the baseline. A decrease in such values indicated relatively greater abduction[1].

The linearity of the sensors embedded in the CyberGlove is 0.62% of maximum nonlinearity over the full range of hand motion and their resolution is 0.5 degrees. These characteristics remain constant over the entire range of motion joint. The output of the transducers is sampled at 12-ms interval.

In order to record movement duration, we used two pressure switches. The first switch was embedded in the hand starting platform (see Figure 2.2.1.1a). When the participants placed their hand on this position, at the beginning of each trial, this switch was pressed. The release of this switch indicated the onset of the reaching movement.

The second switch was placed underneath the to-be-grasped object (see Figure 2.2.1.1a). The weight of the target object maintained the switch pressed whereas the object's lift triggered the switch release. This event determined the end of the reaching movement. Reach duration was taken as the time interval between the release of the first and second switch[2].

2.2.4 Data pre-processing

After data collection, the raw data for all trials for each participant were pre-processed by means of a custom software (Matlab,

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[1] Whereas hand posture was always recorded, results from this measure will be not reported for the Experiments described in Chapters 4 and 6.

[2] Whereas movement duration was always recorded, results from this measure will not be reported for the Experiment described in Chapter 3.

MathWorks, Natick, MA). Specifically, the absolute duration of reaching was first converted in relative terms (as a percentage of movement duration). Then percentage time points were computed in 10 temporal intervals. Within each of these ten intervals, both joints' angular excursions and angular distances were then averaged. An example of the time normalization procedure is represented in Figure 2.2.4.1a-b.

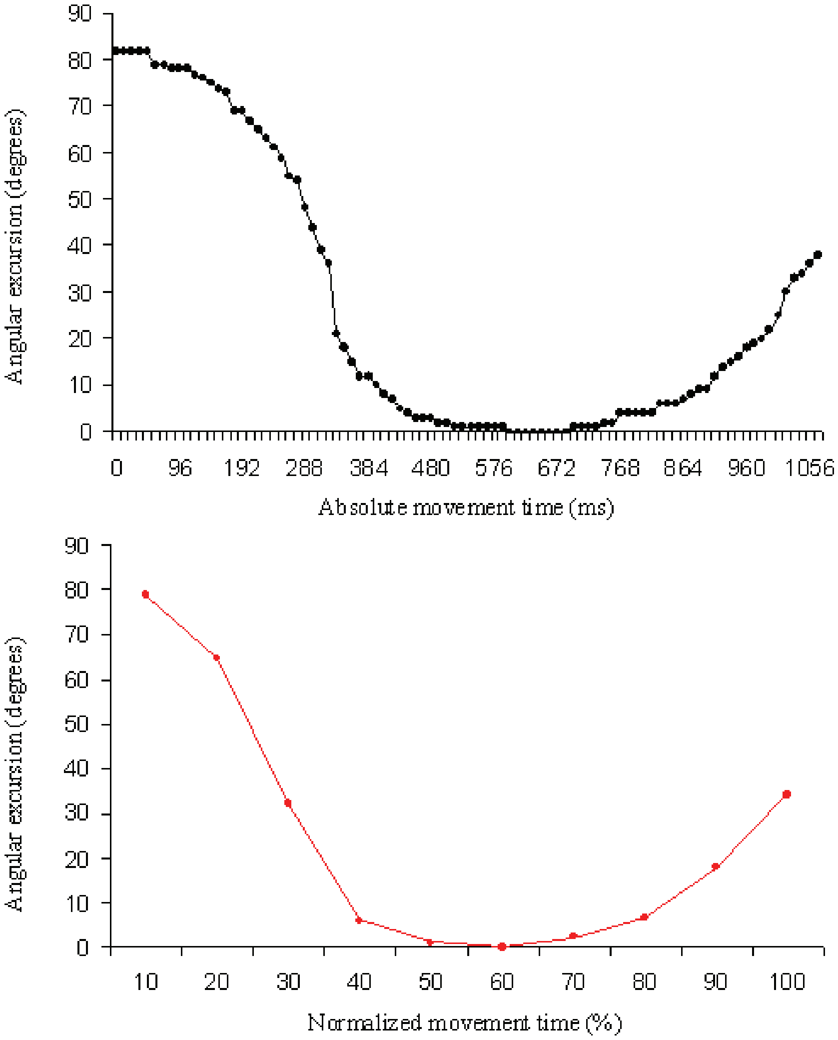

Figure 2.2.4.1 Panel A shows exemplificative data for metacarpal phalangeal joint of the index finger plotted against absolute time. Panel B shows the same data in relative time (%). Please note that the waveform does not differ when expressing kinematic variable against absolute (i.e., milliseconds) and relative (i.e., percentage) reaching time. Since the sampling time for kinematic data recording was constant (i.e., 12 ms; see Paragraph 2.2.3), no curve fitting by interpolation algorithms was requested.

2.2.5 Measures of interest

After time normalization procedures, statistical analyses were performed on the following dependent measures:

1. The absolute duration of reaching movement (milliseconds).

2. Angular excursion recorded at the level of both *mcp* and *pip* joints for thumb, index, middle, ring, and little fingers of the participants' right hand at each epoch of normalized reaching duration (i.e., from 0 to 100%, at step of 10%).

3. The angular distances recorded at the level of adjacent digits' pair of the participants' right hand at each epoch of normalized reaching duration (i.e., from 0 to 100%, at step of 10%).

2.2.6 Data analysis

The measures of interest have been inserted in two types of statistical model: a linear regression and a general linear model. The linear regression model has been applied in order to determine whether the experimental manipulations did affect the degree of motion covariation within the hand during reaching for the visual target. Specifically, I first computed the slope of the regression line (Pearson's coefficient) between angular excursion of 'joint-joint', 'joint-distance', and 'distance-distance' pairs (45, 40, and 6 pairs, respectively, for a total of 91 pairs) for each experimental condition at each epoch of the normalized movement time (from 0 to 100%, at step of 10%). For this analysis, each subject was taken as a statistical unit. Then, in order to obtain a quantitative index of the degree of hand motion covariation, I calculated absolute values of the obtained slopes. Finally, these values were entered into a within-subjects analysis of variance (ANOVA) to test the effect of experimental manipulations on hand motion covariation. For this analysis, each of the 91 pairs was considered as a statistical unit and an alpha level of 0.05 was adopted. Post hoc comparisons were then used to explore the means of interest and false discovery rate (FDR) correction for multiple comparisons was applied (alpha level: $P < 0.01$). Since this analysis provides a quantifiable index of the intrinsic relations amongst fingers (i.e., of the extent to which the motion of digits' single joints is coordinated into synergies) (Santello, Flanders, & Soechting, 2002; Winges, Weber, & Santello, 2003), it has been applied when specifically targeting the investigation of such relation (see Chapter 3).

The general linear model has been applied in order to determine whether the experimental manipulations characterizing each of the experiments reported in the present thesis significantly affected the measures of interest. When specific hypotheses had to be assessed, planned linear contrasts (i.e., vectors that mathematically expressed the predicted results) were implemented. In this respect, one-tailed or two-tailed t-tests (alpha level: $P < 0.05$) were performed for unidirectional or bidirectional hypotheses, respectively (see Chapters 3 and 4). Whereas, when no specific predictions could be made, data were entered into a series of analyses of variance (ANOVAs) (see Chapters 5 and 6). Greenhouse-Geisser correction was applied to the degrees of freedom of F statistics when the Mauchly test showed that the sphericity assumption was violated (alpha level: $P < 0.05$). Post hoc comparisons were then used to explore the means of interest and Bonferroni correction for multiple comparisons was applied (alpha level: $P < 0.05$).

For both the linear regression and the general linear model, the analyses have been carried out by using both Statistical Package for Social Sciences (SPSS) and R software package (http://cran.r-project.org).

2.3 FUNCTIONAL IMAGING INVESTIGATION

2.3.1 Activation paradigm

During the fMRI experiment participants lay supine in the scanner and the task for participants was to observe the presented video-clips. For the entire duration of the movies either odorized or odourless air was delivered. An experimental trial consisted of a single event (i.e., a movie while odorized or odourless air was delivered) which lasted 3 s. The time between the trial offset and the onset of the next trial (i.e., interstimulus interval or ISI) was 10500 ms. If an odour was delivered, an ISI of 10500 ms allowed to recover from any odour adaptation (Hummel et al., 1996). During ISI, a black fixation cross on a blank screen was presented and odourless air was delivered. For each experimental condition, 32 trials were administered in fully randomized order. The experiment consisted of 4 functional runs. Within each of these functional runs, two experimental conditions were presented. Each functional run started with a 18-s rest period consisting of a black fixation cross on a blank screen, ended with a similar rest period of 10500 ms, and lasted 882 s. Consecutive functional runs were intermingled with a 5-minutes break during which no kind of stimulation whatsoever was delivered. By administering two conditions per run, we ensured that signal related to the contrasts of interest spanned frequency bands above the cut-off selected for the high pass filter (see Paragraph 2.3.6 Data analysis). Within each functional run, there was a variable delay of 0-1500-1000-500 ms between trial onset and TR onset for each condition (see Figure 2.3.1.1). Eight of 32 trials were shifted 0 ms with respect to the TR onset, 8 of 32 trials were shifted 1500 ms with respect to the TR onset, 8 of the 32 trials were shifted 1000 ms with respect to the TR onset and 8 of 32 trials were shifted 500 ms with respect to the TR onset (see Figure 2.3.1.1). Such a distribution allowed us to detect the entire evolution of the hemodynamic response associated with an experimental condition with a 500-ms time resolution [when assuming that the evoked hemodynamic response conforms to the canonical hemodynamic response function implemented in SPM 5 (Wellcome Department of Cognitive Neurology, London, www.fil.ion.ucl.ac.uk/spm/)].

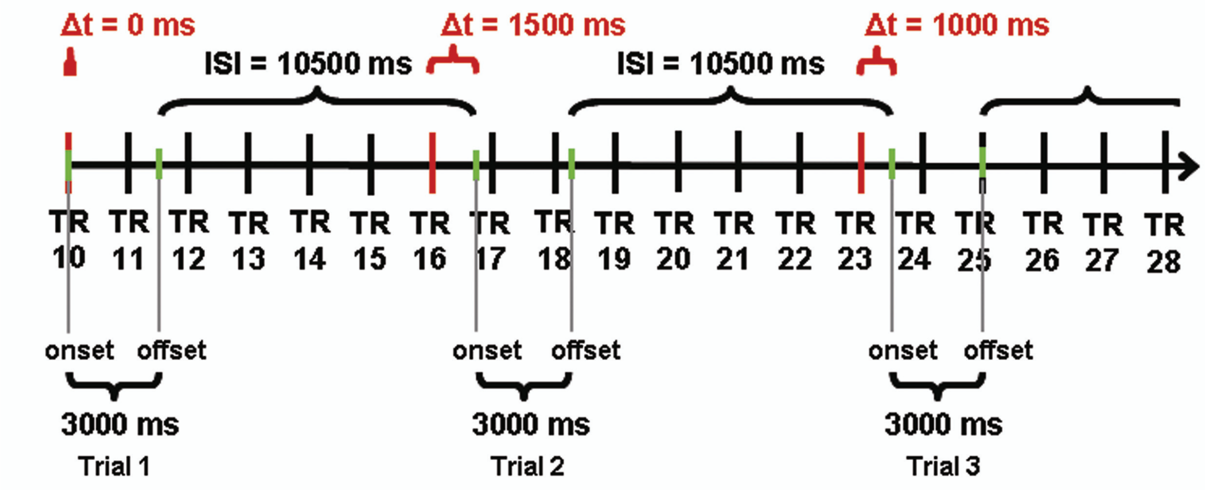

Fig. 2.3.1.1 Graphical representation of the experimental timing. Trial 1 was presented after nine TRs (i.e., 18000 ms) from the beginning of the functional run. Trial 1 onset was shifted 0 ms with respect to the onset of TR 10 (Δt = 0 ms). Following the implementation of a 10500 ms-ISI , the onset for Trial 2 resulted shifted 1500 ms with respect to the onset for TR 16 (Δt = 1500 ms). Then, the 10500 ms-ISI determined a shift in the onset for Trial 3 by 1000 ms with respect to the onset for TR 23 (Δt = 1000 ms). The onset for Trial 4 was shifted 500 ms with respect to the onset for TR 30 (for the sake of brevity, the occurrence of Trial 4 has not been illustrated). Each temporal shift between trial onset and TR onset (Δt = 0-1500-1000-500 ms) was repeated eight times during the entire functional run for a total of 32 trials.

2.3.2 Stimuli and apparatus

Both the video-clips (Audio Video Interleave format, 25 frames/s, resolution 400 × 300 pixel; duration 3s) and the olfactory stimulation were presented by using the software called Presentation (Neurobehavioral Systems, Albany, CA, www.neuro-bs.com) which ensured synchronization with the MR scanner. An LCD computer-controlled projector (NEC, resolution 1024 × 768, refresh rate 60 Hz) was employed to present the movies in colour at the centre of a screen positioned outside the bore of the magnet. The movies were viewed by the participants through a mirror mounted on the head coil. When projected onto the 10 mirror, the movies were 26.8 cm wide × 20.1 cm high and subtended visual angles of 20 deg × 15 deg. The video-clips represented a human right hand either in the absence or in the presence of an object. The hand either performed a grasp movement or rested in a prone position. The object was signalled via either vision or olfaction or through both vision and olfaction. In this respect, the four different fruits which have been already used for the kinematical experiments (see Figure 2.2.1.1b) were adopted as visual objects. Similarly, the four different odours which have been already utilized for the kinematical investigations were adopted as olfactory objects (see Paragraph 2.2.2 Stimuli and apparatus). Since the computer-controlled olfactometer which have been employed for the kinematical experiments (see Paragraph 2.2.2 Stimuli and apparatus) was MRI compatible (i.e., it did not present ferromagnetic components), I used this device to deliver olfactory stimulation to participants lay in the MR scanner.

2.3.3 Odour recognition task and paced-breathing session

In order to ensure that participants were able to identify each of the four delivered odours (i.e., orange odour, apple odour, strawberry odour, and almond odour), we asked to participants to perform an odour recognition task. Before entering within the scanner, volunteers were presented with the four visual objects (see Figure 2.2.1.1b). Then, an odour was presented for two seconds and participants were instructed to indicate the object associated with that odour. A total of eight trials (two for each type of odour) was presented in randomized order. When performing the task, participants showed no errors. Further, in the present study we decided to adopt four odours which were judged to have equal intensity, hedonic tone and familiarity in previous investigations (Tubaldi, Ansuini, Tirindelli, & Castiello, 2008a).

Before the experiment started, participants took part in a paced-breathing session. During this session, participants were trained to synchronize their breathing cycle according to the rhythm with which odour would have been delivered during the fMRI experiment. They performed 15 paced air inhalations within one training block lasting 210 s (for technical details see Tabert et al., 2007). This ensured that odour administration during the fMRI experiment was always synchronized with the participants' inhalation phase and that the sampling of the delivered odour was uniform across scans and participants.

2.3.4 Data acquisition

Gradient echo, T2*-weighted echoplanar images (EPI) with blood-oxygen level-dependent (BOLD) contrast were acquired on a 3T Siemens Magnetom Trio MRI scanner equipped with a 12-channel head array radio-frequency coil. EPI datasets with whole brain coverage (32 transversal slices; 3 × 3 × 3.5 mm voxel size; 0.7 mm gap) were collected in interleaved fashion every 2000 ms with the following parameters: field-of-view, 192 × 192 mm; in-plan resolution 64 × 64 voxels; echo time, 33 ms; bandwidth, 2442 Hz/Px. For each functional run, a total of 441 volumes was collected, minus 5 'dummy' volumes to permit T1 equilibration. In addition, high-resolution T1-weighted images (anatomical scans) were acquired for each participant (MP-RAGE, 160 sagittal slices, in-plane resolution 224 × 256 voxels, 1 mm isotropic voxels, TR = 2300 ms, TE = 3 ms).

2.3.5 Data pre-processing

MRI data were processed using Statistical Parametric Mapping software (SPM 5, Wellcome Department of Cognitive Neurology, London, www.fil.ion.ucl.ac.uk/spm/), implemented in Matlab 7.0 (Mathworks Inc., USA, www.mathworks.com). First, EPI images were realigned to the first functional volume of each run in order to correct for any head movement occurring within the run. Second, high quality T1 images were co-registered to the mean EPI image and segmented. The coregistered grey matter segment was normalized onto the grey matter template (available in the SPM 5 'apriori' directory), and the resulting normalization parameters applied to all EPI images (re-sampled voxels at 2 × 2 × 2 mm). The T1 image was also normalized to the MNI space using the same parameters, keeping the original resolution of 1 × 1 × 1 mm. Finally, EPI data were spatially smoothed adopting an 8 mm FWHM (Full Width at Half Maximum) Gaussian kernel.

2.3.6 Data analysis

The event-related functional data were analyzed using the general linear model (Friston et al., 1995). A regressor of interest corresponding to each experimental condition was defined based on the timing of presentation for the experimental condition (duration = 3 s). These functions were convolved with a canonical hemodynamic response function. Subject-specific movement parameters were included to account for translation and rotation along the 3 possible dimensions as measured during the realignment stage. A high pass filter (cut-off, 128 s) was also applied to remove low-frequency drifts in signal. The parameter estimates for each regressor were calculated for all brain voxels (i.e., beta images were computed). Then, beta images referring to each experimental condition were extracted for each subject and entered into a within-subjects flexible factorial design. A third factor of no interest was also modelled, i.e., the effect of subjects. The present procedure permitted to ascertain which brain areas were sensitive to the experimental manipulations and how different experimental conditions did affect activity within these areas.

2.3.7 Localization

Anatomical details of significant signal changes were obtained by superimposing the SPM{t} maps resulting from the performed analyses on the T1 canonical MNI template image. Results were also checked against the normalized structural images for each participant. For the purpose of additional anatomical precision, the SPM{t} map were overlaid on a surface based-representation of the MNI canonical brain using the SPM surfrend toolbox (written by I. Kahn; http://spmsurfrend.sourceforge.net). The surface-based representation was then rendered using FreeSurfer (CorTechs Labs, Inc., Charlestown, MA) (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999). We used 2 atlases as general neuroanatomical reference

(Duvernoi & Bourgouin, 1999; Mai, Assheuer, & Paxinos, 2004). Further, the SPM Anatomy Toolbox 1.6 (Eickhoff et al., 2005) based on 3-dimensional probabilistic cytoarchitectonic maps was used to determine the cytoarchitectonic probability (where available) of peak activity voxels. For the premotor cortices we also ascertained the position of the activation clusters and peaks from a meta-analysis by Mayka, Corcos, Leurgans, & Vaillancourt (2006). Activation peaks were reported in MNI coordinates.

3. The grasping side of odours[3]

Abstract

Crossmodal links between vision, audition, proprioception, and the sense of touch during natural tasks such as hand grasping movements have been identified. However, how olfaction contributes to plan and control hand grasping movements has not been decisively shown. We used kinematics to explicitly test the influence of olfactory stimuli on hand grasping movements. Participants were requested to reach towards and grasp a small or a large visual target (i.e., precision grip, involving the opposition of index finger and thumb for a small size target and whole hand grasp, involving the flexion of all digits around the object for a large target) in the absence or in the presence of an odour evoking either a small or a large object that if grasped would require a precision grip and a whole hand grasp, respectively. When the type of grasp evoked by the odour did not coincide with that for the visual target, interference effects were evident on the kinematics of hand shaping and the level of synergies amongst fingers decreased. When the visual target and the object evoked by the odour required the same type of grasp, facilitation emerged and the intrinsic relations amongst individual fingers were maintained.

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3.1 INTRODUCTION

An aspect which has been largely neglected in terms of the multisensory processes underlying hand grasping movements concerns chemosensory information. To date, only one study performed in our laboratory considered reach-to-grasp movements performed towards a visual target-object in the presence of an olfactory stimulus (Castiello, Zucco, Parma, Ansuini & Tirindelli, 2006). The olfactory stimulus could evoke an object of a smaller or larger dimension than the visual target-object. In these circumstances, the maximum distance between the index finger and thumb (i.e., maximum hand aperture) was affected. If the olfactory stimulus evoked an object smaller than the target-object, then maximum hand aperture was smaller than when no odour was delivered. If the olfactory stimulus evoked an object larger than the target-object, then maximum hand aperture was larger than when grasping occurred in the absence of olfactory information (Castiello et al., 2006). Although suggestive of the potential influence olfactory information may have on hand grasping movements, the dependent measure used in this preliminary observation (i.e., maximum hand aperture) did not allow for a precise examination of three critical aspects.

First, it does not permit a full understanding of how detailed the motor commands embedded within the 'grasp' plan elicited by the object's olfactory representation are. In this respect, recording detailed kinematics at the level of individual digits may shed more light on this aspect. If the motion of individual fingers is modulated by the olfactory information, then the 'grasp' plan elicited by the olfactory representation may consider the structure of the object associated with the odour. Second, maximum hand aperture is a measure which does not allow to ascertain how olfactory interference fully manifests within a complex sensory-motor system such as that subserving visual grasping. An index quantifying the intrinsic relations amongst fingers, such as the pattern of hand motion covariation, may be needed. If an odour affects the pattern of hand motion covariation, then olfactory-induced destabilization of motion synergies amongst fingers would be a potent index of interference (Santello et al., 2002; Winges et al., 2003). Conversely, if an odour leaves unchanged the pattern of hand motion covariation, then no inferences about olfactory type of interference could be drawn. Finally, maximum hand aperture is a time-locked kinematic parameter (i.e., occurs at 50–60% of reaching duration when grasping under natural conditions) which does not allow to determine with a high temporal resolution when the olfactory and the visual information integrate en-route for action control. In this respect, by looking at the entire time course of action would allow to determine when the olfactory and the visual information do integrate.

With this in mind, we set out to investigate detailed hand kinematics along the entire time course of a reach-to-grasp movement towards visual targets of different size either in the absence or in the presence of preceding olfactory information. Capitalizing on the effects of olfactory information on hand grasping movements previously reported (Castiello et al., 2006), we expected that an odour delivered before movement initiation might be able to trigger a 'grasp' plan reflecting the size of the object associated with the odour. To elaborate, an odour evoking a large object would elicit the type of grasp people naturally adopt for acting upon that object, i.e., a whole hand grasp (WHG). Whereas, an odour evoking a small object would elicit a precision grip (PG), i.e., the appropriate 'grasp' plan for interact with a small size object. In this respect, we hypothesised that when the odour-evoked object has the same size of the visual target, the 'grasp' plan elicited by the olfactory stimulus should magnify the 'grasp' plan elicited by the visual target. This is because the odour triggers an object that if grasped would require the same type of grasp as the visual target. Conversely, when the odour-evoked object has a different size than the visual target, the 'grasp' plan dictated by the olfactory stimulus should interfere with the 'grasp' plan dictated by the visual target. Crucially, under these circumstances, interference concerning with motion synergies amongst fingers should also be found. This is because the odour elicits an object that if grasped would require a different type of grasp as the visual target.

3.2 METHODS

3.2.1 Participants

Twenty-six right handed subjects (21 females and 5 males, mean age 2263.5 years) took part in the experiment (see Chapter 2). The experimental session lasted approximately 30 min.

3.2.2 Procedures

The task for participants was to reach, grasp and lift a visual target-object either in the absence or in the presence of an olfactory stimulus (see Chapter 2). This task could be performed under six different conditions:

1. Odourless air-Large target (i.e., OL) condition. Odourless air was delivered before the hand grasp movement towards a large target was initiated.

2. Odourless air-Small target (i.e., OS) condition. Odourless air was delivered before the hand grasp movement towards a small target was initiated.

3. Large odour-Large target (i.e., LL) condition. An odour associated with an object of a large size was presented before the hand grasp movement towards a large target was initiated.

4. Small odour-Small target (i.e., SS) condition. An odour associated with an object of a small size was presented before the hand grasp movement towards a small target was initiated.

5. Small odour-Large target (i.e., SL) condition. An odour associated with an object of a small size was presented

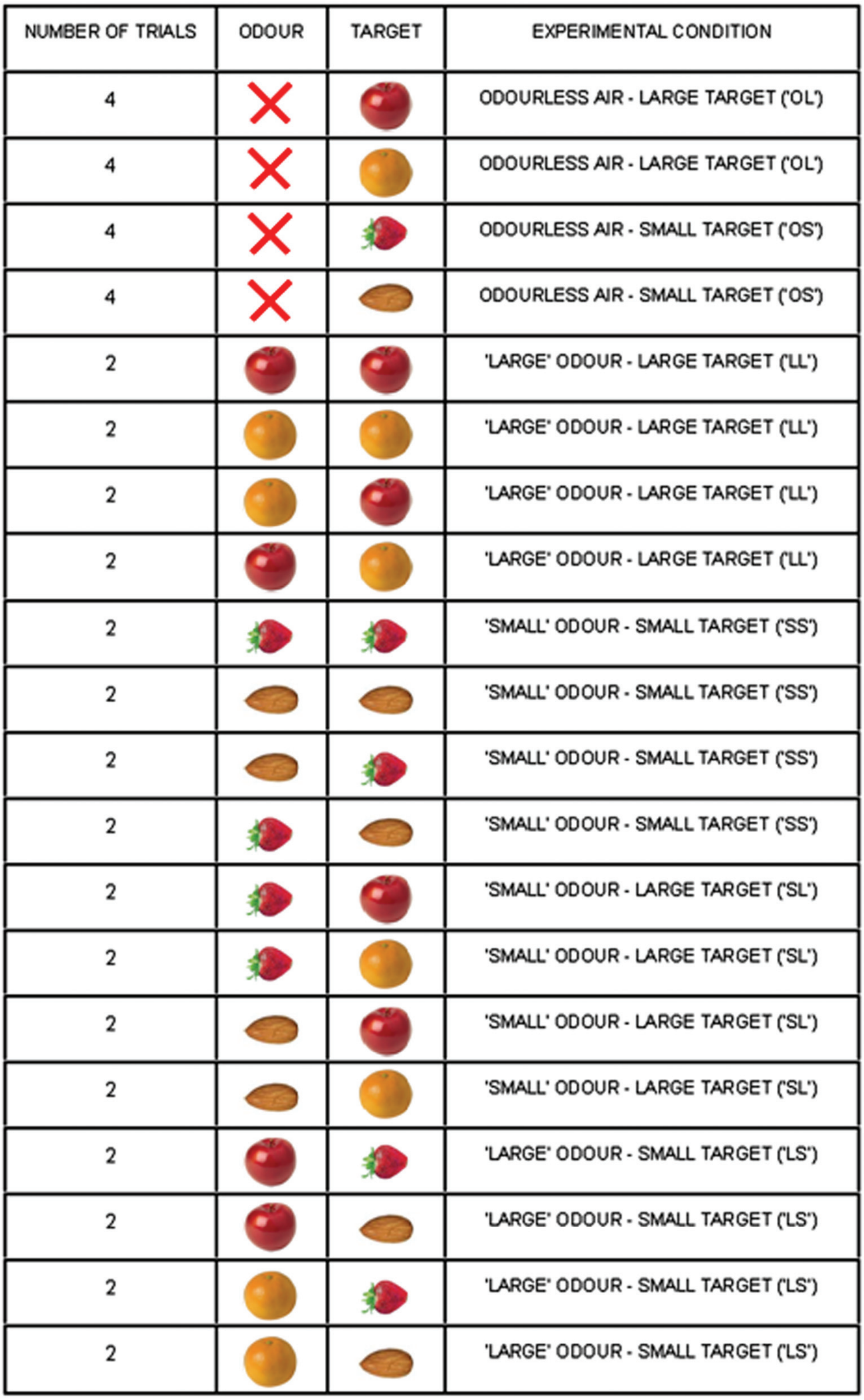
before the hand grasp movement towards a large target was initiated.

6. Large odour-Small target (i.e., LS) condition. An odour associated with an object of a large size was presented before the hand grasp movement towards a small target was initiated.

Odour/target combinations for each experimental condition are represented in Figure 3.2.2.1. Participants performed a total of 48 trials (8 for each experimental condition) which were presented in randomized order within one block.

3.2.3 Stimuli and apparatus

Stimuli and apparatus adopted in the present experiment have been described within the ‘General methods’ section (see Chapter 2).



NUMBER OF TRIALS	ODOUR	TARGET	EXPERIMENTAL CONDITION
4	✗	🍎	ODOURLESS AIR - LARGE TARGET ('OL')
4	✗	🍊	ODOURLESS AIR - LARGE TARGET ('OL')
4	✗	🍓	ODOURLESS AIR - SMALL TARGET ('OS')
4	✗	🌰	ODOURLESS AIR - SMALL TARGET ('OS')
2	🍎	🍎	'LARGE' ODOUR - LARGE TARGET ('LL')
2	🍊	🍊	'LARGE' ODOUR - LARGE TARGET ('LL')
2	🍊	🍎	'LARGE' ODOUR - LARGE TARGET ('LL')
2	🍎	🍊	'LARGE' ODOUR - LARGE TARGET ('LL')
2	🍓	🍓	'SMALL' ODOUR - SMALL TARGET ('SS')
2	🌰	🌰	'SMALL' ODOUR - SMALL TARGET ('SS')
2	🌰	🍓	'SMALL' ODOUR - SMALL TARGET ('SS')
2	🍓	🌰	'SMALL' ODOUR - SMALL TARGET ('SS')
2	🍓	🍎	'SMALL' ODOUR - LARGE TARGET ('SL')
2	🍓	🍊	'SMALL' ODOUR - LARGE TARGET ('SL')
2	🌰	🍎	'SMALL' ODOUR - LARGE TARGET ('SL')
2	🌰	🍊	'SMALL' ODOUR - LARGE TARGET ('SL')
2	🍎	🍓	'LARGE' ODOUR - SMALL TARGET ('LS')
2	🍎	🌰	'LARGE' ODOUR - SMALL TARGET ('LS')
2	🍊	🍓	'LARGE' ODOUR - SMALL TARGET ('LS')
2	🍊	🌰	'LARGE' ODOUR - SMALL TARGET ('LS')

Figure 3.2.2.1 Odour/target combination for each experimental condition. From left to right, columns report the number of trials for each odour/target combination, the type of odour, the type of target, and the experimental conditions.

3.2.4 Data analysis

In order to asses the experimental hypotheses, we first tested whether the angular pattern for all digits' joints and distances differed for a large than for a small visual target in the absence of odour (see Chapter 2). This is an important aspect of the present study because in order to ascertain the effects of olfactory information in terms of 'size' on hand shaping, it is necessary to demonstrate that the size of the visual target does affect hand shaping. Then, we ascertained the magnification of the pattern of fingers' joints and distances when the size of the odour-evoked object did match the size of the visual target. In this respect, we tested whether angular values for all fingers' joints and distances indicated (*i*) a greater fingers' extension and abduction, respectively, for the LL than for the OL condition and (*ii*) a greater fingers' flexion and adduction, respectively, for the SS than for the OS condition (see Chapter 2). Subsequently, we evaluated the interference effects when the size of the odour-evoked object did not match the size of the visual target. In this respect, we tested whether angular values for all fingers' joints and distances indicated: (*iii*) a greater fingers' flexion and adduction, respectively, for the SL than for the OL condition and *iv*) a greater fingers' extension and abduction, respectively, for the LS than for the OS condition (see Chapter 2). All the experimental hypotheses were assessed at each epoch of the normalized movement time (from 10 to 100% of reaching duration, at step of 10%) by means of planned contrasts (see Chapter 2). We used one-tailed t-tests for all fingers' joints and distances since the aforementioned effects had a specific direction (see Chapter

2). Whereas, two-tailed t-tests was used for the thumb's joints given that on the basis of recent experimental evidence no specific predictions regarding the direction of the 'size' effect could be made (Frak, Paulignan, & Jeannerod, 2001; Ansuini, Santello, Tubaldi, Massaccesi, & Castiello, 2007) (see Chapter 2). This is because it has been demonstrated that the thumb's angular excursion is not specifically modulated to object's structural properties, but it reflects a role in action guidance. Finally, in order to asses the influence that olfactory information may have on the unfolding of hand shaping, we tested whether the hand motion covariation pattern varied across the six experimental conditions (see Chapter 2). In this respect, the absolute value of the slopes of the regression lines fitting angular values between articulations' pairs computed for each experimental condition at each epoch of the normalized movement time was entered into an ANOVA with odour 'size' (large, small, and no-odour), target size (large, small), and time (from 10 to 100%, by step of 10%) as within-subjects factors (see Chapter 2). Post hoc comparisons were then used to explore the means of interest (see Chapter 2).

3.3 RESULTS

3.3.1 The effect of size on hand shaping

Participants naturally grasped the large visual target opposing the thumb with all the other fingers (i.e., by using a WHG), and the small visual target between the thumb and either (or both) the index and the middle fingers (i.e., by using a PG).

Now I present the effects of target size on hand shaping as derived from the conditions in which the visual targets are presented in the absence of preceding olfactory information. In this respect, significantly different kinematic patterns of hand shaping for the small and the large targets were found. As shown in Figure 3.3.1.1, the *mcp* joint for the thumb was more extended for the large than for the small target from 40% to the end of the movement. The *mcp* joint for the index and the middle fingers was significantly more extended for the large than for the small target throughout the entire movement. For the ring and little fingers no significant differences with respect to target size were found from 70% and from 40% up to the end of movement duration, respectively (see Figure 3.3.1.1). A similar pattern was also evident for the *pip* joints of all fingers (except for the thumb), but differences related to target size became evident at a later time than for the *mcp* joints. The *pip* joint of the thumb was more flexed for the large than for the small target during the last epoch (90-100%). The thumb-index abduction angle was greater for the large than for the small target from 30 up to 100% of movement duration (see Figure 3.3.1.2). Similar size effects were also evident for the middle-ring and the ring-little abduction angles from 10 to 40% of movement duration (see Figure 3.3.1.2). In summary, the fingers were more extended when preparing to grasp a larger than a smaller target whereas the thumb was more flexed for the large than for the small target. This signifies that the size of the visual target was taken into account when planning the motion of all digits.

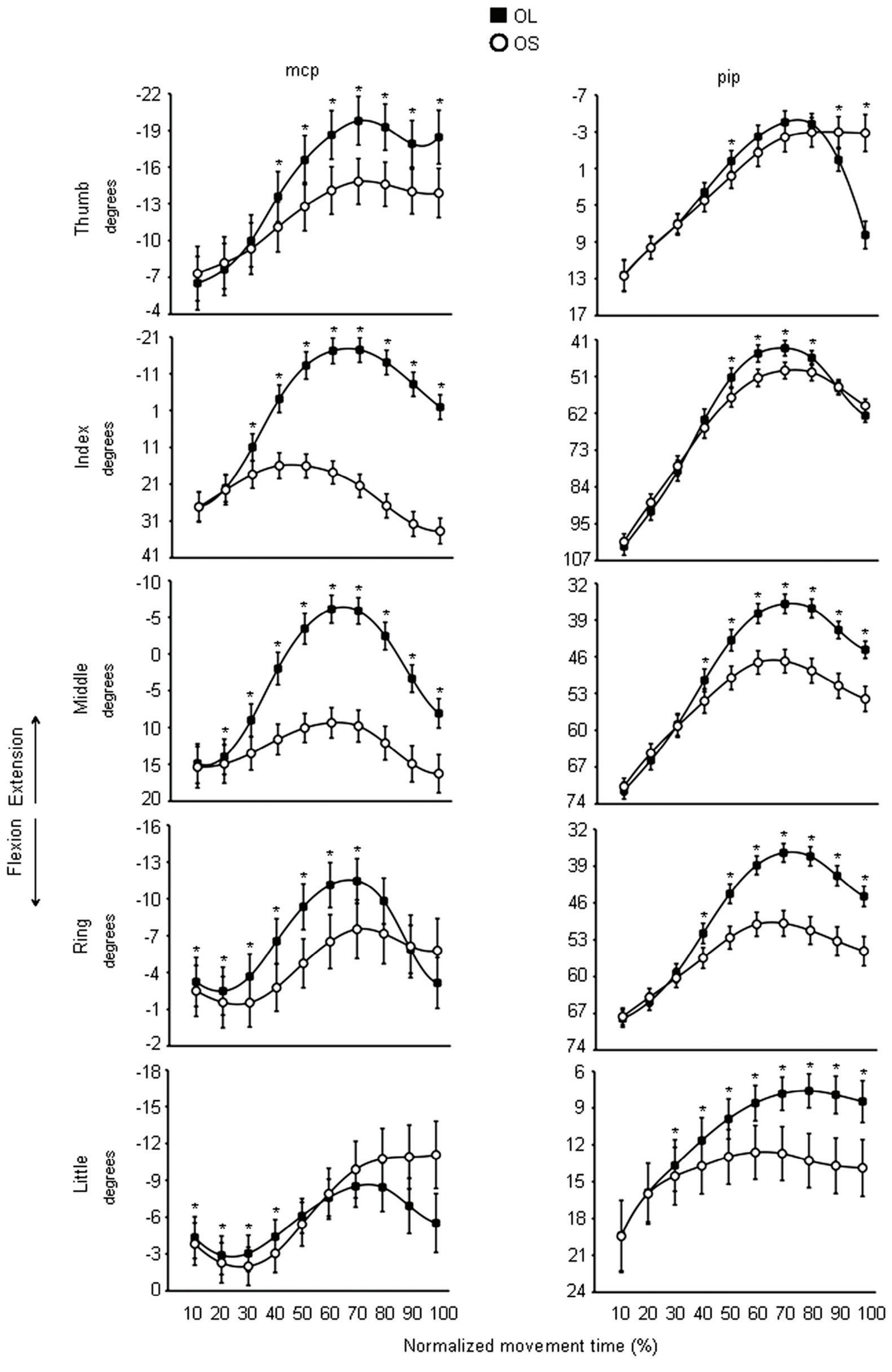


Figure 3.3.1.1 Time course of fingers motion during reaching in the absence of olfactory stimuli. Each trace corresponds to the average angular excursion for the *mcp* (left panels) and *pip* (right panels) joints of the thumb, index, middle, ring, and little fingers for the OL (black squares) and the OS (white circles) conditions. Bars represent mean standard error. Positive values correspond to finger flexion, whereas negative values correspond to finger extension. Asterisks indicate significant results ($P < 0.05$) for the comparisons between the OL and the OS conditions at different epochs of normalized movement time. OL = Odourless air-Large target; OS = Odourless air-Small target.

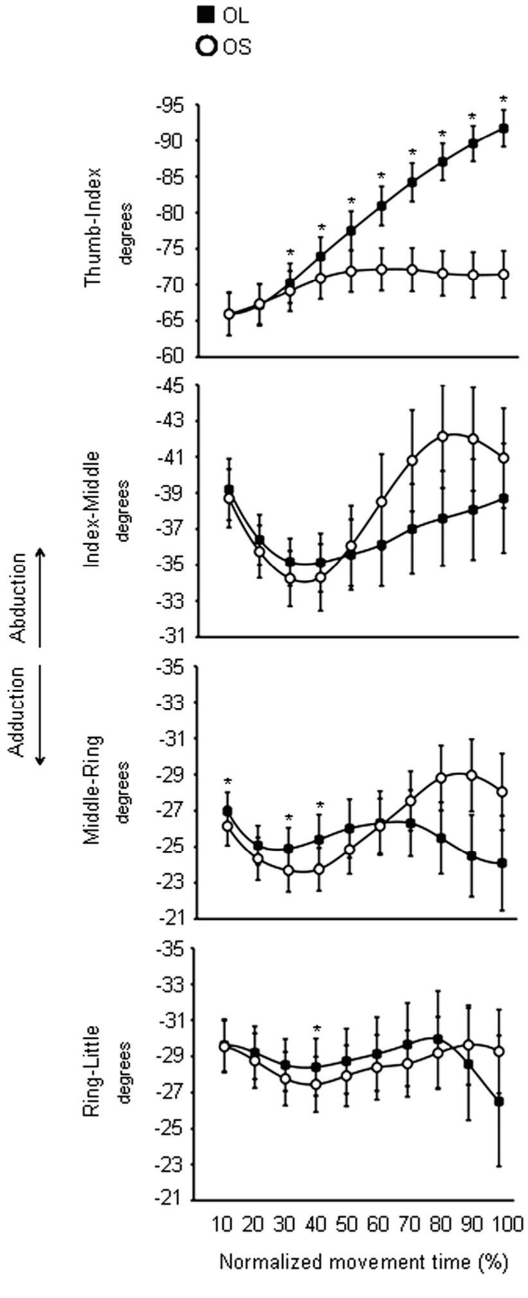


Figure 3.3.1.2 Time course of angular distance between fingers during reaching in the absence of olfactory stimuli. Each trace corresponds to the average angular distance for the OL (black squares) and the OS (white circles) conditions. Bars represent mean standard error. Increase in negative values correspond to bigger abduction (i.e., increase of digits' angular distance). Asterisks indicate significant results ($P < 0.05$) for the comparisons between the OL and the OS conditions at different epochs of normalized movement time. OL = Odourless air-Large target; OS = Odourless air-Small target.

3.3.2 The effect of odours on hand shaping

Here we describe the specific effects of odour 'size' on hand shaping. Specifically in the following sections we report on the effects of odour 'size' on the angular excursion for all digits' joints and distances.

Grasping a large target. For the LL condition, the *pip* joint of the index, middle and ring fingers was more extended than for the OL condition (see Figure 3.3.2.1). This effect was particularly evident at the very beginning of movement duration (i.e., at 10-20% for both the index and the ring finger, and at 20% for the middle finger) (see Appendix A). A similar effect was exhibited by the *mcp* joint of the thumb which was more extended for the LL than for the OL condition at 20% of movement duration (see Figure 3.3.2.1 and Appendix A). For these joints, after 20% of movement duration, no differences when comparing the LL and the OL conditions were evident. For the SL condition, the *mcp* joint of the index, middle, and ring fingers was more flexed than for the OL condition (see Figure 3.3.2.2). In particular, the *mcp* joint of index, middle, and ring fingers showed an over-flexion at about half of movement duration (see Appendix A). However, a delayed odour 'size' effect was evident for the *mcp* joint of the index finger (see Appendix A). A similar pattern was also found for the *pip* joints of both the thumb and the index finger showing a greater flexion in the SL than in the OL condition at 50% and 40% of movement duration, respectively (see Figure 3.3.2.2 and Appendix A). The middle-ring and the ring-little distances showed an over-adduction for the SL than for the OL condition. This effect was evident within the second half of movement duration (see Figure 3.3.2.3 and Appendix B).

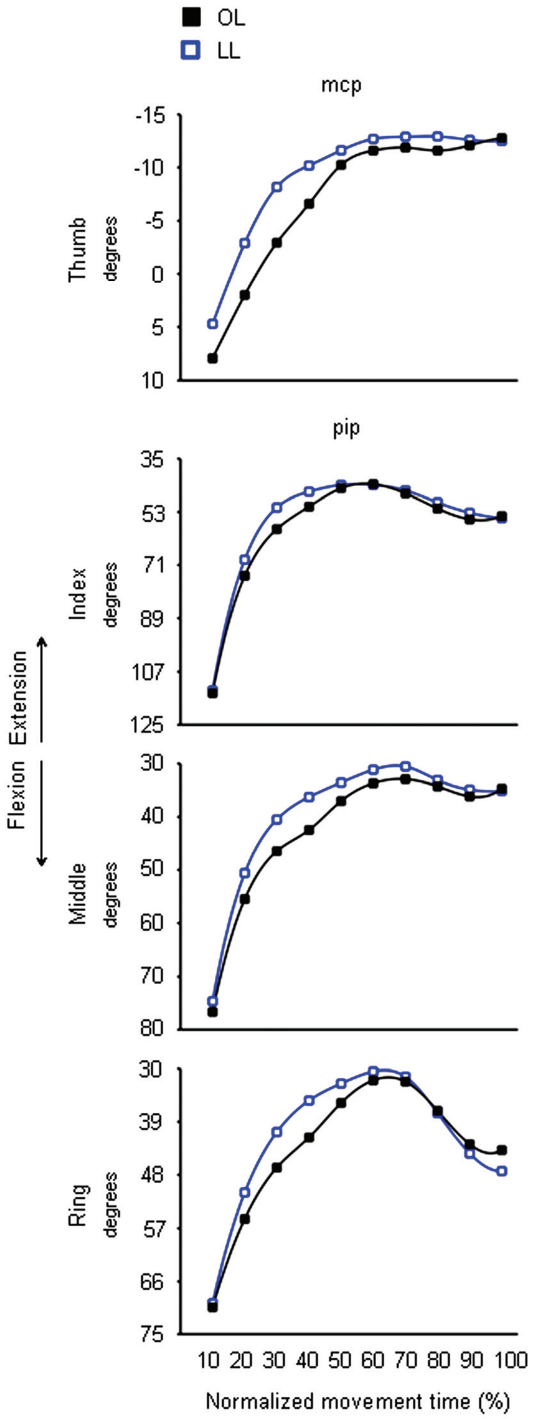


Figure 3.3.2.1 Time course of finger motion during reaching for the large target either in the absence or in the presence of an odour evoking a large object. Each trace corresponds to the average angular excursion of a representative subject (Subject 15) for the *mcp* joint of the thumb and the *pip* joint of the index, middle, and ring fingers when performing the OL (black squares) and the LL (blue squares) conditions. Positive values correspond to finger flexion whereas negative values correspond to finger extension. OL = Odourless air-Large target; LL = Large odour-Large target.

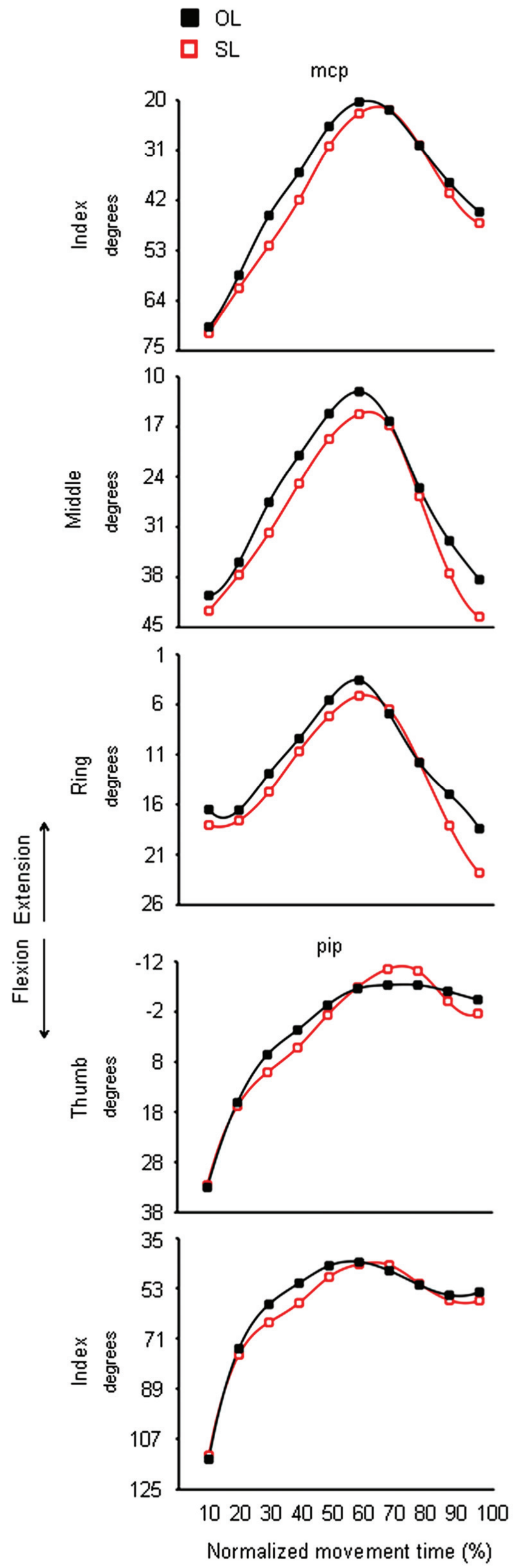


Figure 3.3.2.2 Time course of finger motion during reaching for the large target either in the absence or in the presence of an odour evoking a small object. Each trace denotes the average angular excursion of a representative subject (subject 15) for the *mcp* joint of index, middle and ring fingers (upper panels), and the *pip* joint of the thumb and index finger (lower panels) when performing the OL (black squares) and the SL (red squares) conditions. Positive values correspond to finger flexion whereas negative values correspond to finger extension. OL = Odourless air-Large target; SL = Small odour-Large target.

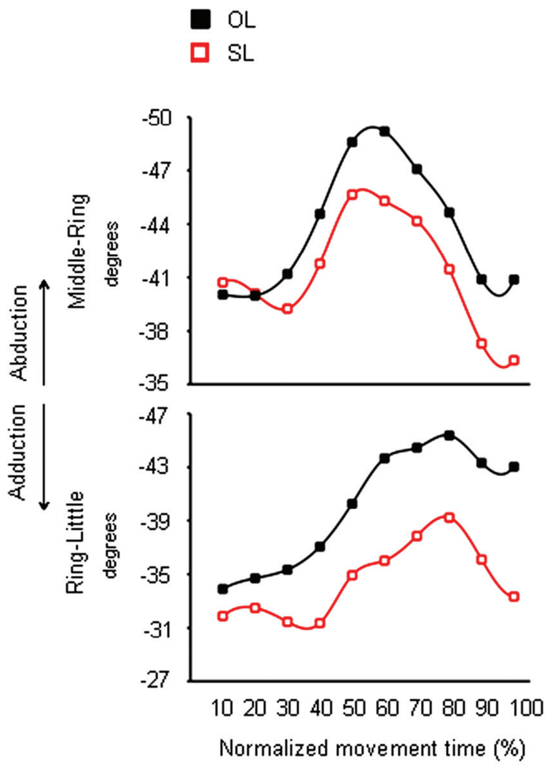


Figure 3.3.2.3 Time course of angular distance between fingers during reaching for the large target either in the absence or in the presence of an odour evoking a small object. Each trace denotes average angular distance of a representative subject (Subject 10) for the middle-ring and the ring-little fingers when performing the OL (black squares) and the SL (red squares) conditions. Increase in negative values correspond to bigger abduction (i.e., increase of digits' angular distance). OL = Odourless air-Large target; SL = Small odour-Large target.

These results indicate that the presence of a 'large' odour magnified the extension pattern which was found when a large target was grasped in the absence of olfactory information. Such magnification was particularly evident during the first part of movement duration. Conversely, the presence of a 'small' odour determined a flexion pattern which was not evident when the large target was grasped in the absence of olfactory information (showing a similarity, in terms of flexion, with the pattern elicited by the small target when grasped in the absence of olfactory information). The effect due to the presence of the 'small' odour persisted up to the end of the movement duration.

Grasping a small target. For the SS condition, the *mcp* joints of both the index and the little finger were more flexed than for the OS condition. Specifically, the *mcp* joints for both the index and the little finger showed such over-flexion at 40%, and from 20 up to 60% of movement duration, respectively (see Figure 3.3.2.4 and Appendix C).

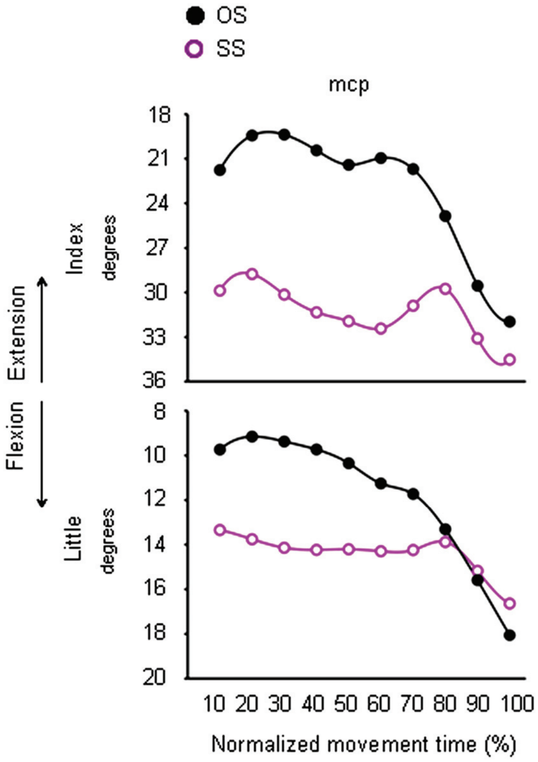


Figure 3.3.2.4 Time course of finger motion during reaching for the small target either in the absence or in the presence of an odour evoking a small object. Each trace denotes average angular excursion of a representative subject (Subject 2) for the *mcp* joint of the index and the little fingers when performing the OS (black circles) and the SS (purple circles) conditions. Positive values correspond to finger flexion whereas negative values correspond to finger extension. OS = Odourless air-Small target; SS = Small odour-Small target.

For the LS condition, angular excursion of the *mcp* joint for both the thumb and the ring finger significantly differed from angular excursions obtained for the OS condition. In particular, at 20% of movement duration, the *mcp* joint of the ring finger was more extended for the LS than for the OS condition (see Figure 3.3.2.5 and

Appendix C). In contrast, from 10% up to the end of movement duration, the *mcp* joint of the thumb was more flexed for the LS than for the OS condition (see Figure 3.3.2.5 and Appendix C).

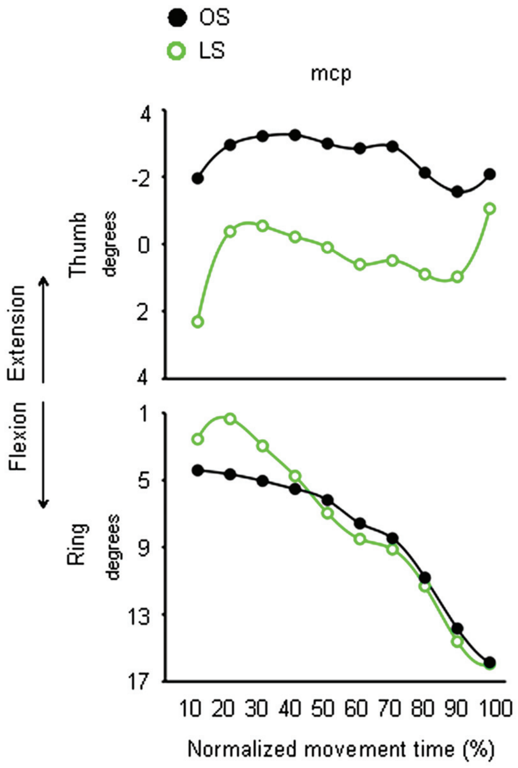


Figure 3.3.2.5 Time course of finger motion during reaching for the small target either in the absence or in the presence of an odour evoking a large object. Each trace depicts average angular excursion of a representative subject (Subject 2) for the *mcp* joint of the thumb and the ring finger when performing the OS (black circles) and the LS (green circles) conditions. Positive values correspond to finger flexion whereas negative values correspond to finger extension. OS = Odourless air-Small target; LS = Large odour-Small target.

To sum up, the presence of a ‘small’ odour enhanced the pattern of hand flexion which was found when the small target was grasped in the absence of olfactory information. Such intensification was particularly evident during the first part of movement duration. Conversely, the presence of a ‘large’ odour determined both a greater ring finger extension and a greater thumb flexion with respect to when the small target was grasped in the absence of olfactory information (showing similarity with the pattern elicited by the large target when grasped in the absence of olfactory information). The effect due to the presence of the 'large' odour persisted throughout the entire movement duration.

3.3.3 Hand motion covariation

This section reports on the results concerned with the pattern of hand motion covariation as obtained by the absolute value of the slopes of the regression lines fitting angular values between articulations' pairs. The relationship between the size of the odour-evoked object and the size of the visual target did affect the absolute value of the slopes during reaching (three-way interaction: $F_{(6.36,572.25)} = 4.02$, $P < 0.001$). Post-hoc analyses revealed that the slope absolute values decreased at specific epochs during reaching only when the odour was associated with an object having a different size than the visual target (see Appendix D). Further, the temporal window of the reduction in covariation was wider when the stimulus associated with the odour was small rather than large (see Appendix D). Therefore, the pattern of hand motion covariation was weakened when the 'size' of the odour did not match the size of the target. Importantly the delivery of an odour evoking an object of a similar size to the target did not alter the motion covariation characterizing the hand when no odour was delivered.

3.4 DISCUSSION

The present study has investigated the effects of odour stimuli on the kinematics of hand shaping at the level of individual digits' motion. The results indicate that the kinematic patterning of a reach-to-grasp movement was influenced by the 'size' of an odour. Crucially, the motor plan evoked by the odour is surprisingly fine grained and when elicited can modulate both the pattern of angular excursion at the level of individual fingers' joints and the degree of synergic movement amongst digits.

3.4.1 When the olfactory 'size' do not match the visual 'size' interference emerges

As reported here, hand grasping movements can be planned on the basis of olfactory information. The motor plan elicited by the olfactory stimulus is not totally overridden by the motor plan triggered, at a later time, by the visual target. That is, some aspects of the motor plan elicited by a 'size' incongruent olfactory stimulus persist in the motor plan executed for grasping the visual target. This effect was evident when comparing the incongruent odour (LS and SL) with the respective odourless conditions (OS and OL).

When the odour was 'large' and the visual target was small, only one finger joint (i.e., the *mcp* joint of the ring finger) was affected by the olfactory stimulus. In contrast, the influence of the 'small' odour on the kinematics of a hand grasp movement towards a large target was much more evident and a greater number of joints were mobilized. This seems to suggest that planning for a reach-to-grasp movement on the basis of a ‘small’ odour when the target is large poses more constraints than when the odour is ‘large’ and the movement is directed towards a small target. Our proposal is that the motor plan elicited by the odour has to be modified according to the visual target. However such reorganization could be more easily managed without compromising object grasp when the odour is ‘large’ and the visual target is small than vice versa.

In terms of complexity, several factors could contribute to the difference in kinematic response between the two types of incongruent conditions. For instance, biomechanically there may be more advantage for closure (as happens for the present LS condition) than for opening (as happens for the present SL condition). Colebatch & Gandevia (1989) found, for example, that thumb and finger flexors were 2.8-3.5 times stronger than extensors. For a task focused upon a grasping action, the biomechanical setting for the flexors would be more favoured. This view seems to be supported by the results obtained in previous studies looking at the reprogramming of grip aperture following a perturbation of object size (Castiello, Bennett, & Stelmach, 1993; Bock & Jungling, 1999). These findings indicate that the passage from a large to a small object was easier than the passage from a small to a large object.

Of note is the finding that when the odour is ‘large’ and the target is small, the thumb is over-flexed with respect to the condition in which the small visual target-object is presented without preceding olfactory information. A possible explanation for such an effect considers how the thumb behaves for movements performed in the absence of olfactory information (i.e., odourless air conditions). In such circumstances, the thumb is usually more flexed at the end of the movement for the large than for the small target. Therefore, the finding that a 'large' odour determines an over-flexion of this digit strengthens the hypothesis that a 'grasp' plan suited for acting upon a larger target is evoked by the odour.

The delivery of 'incongruent' odours had an effect also on the extent of synergic movements within the hand. This is signified by the loosening of synergies amongst fingers observed for the incongruent odour conditions with respect to the level of synergies observed for the odourless air conditions. A possible interpretation for these findings relies on the requirement to integrate the 'grasp' plan established for the visual target into the motor plan elicited by the preceding odorous stimulus. This integration process is gradual and it spreads throughout the entire movement duration. In other words, the 'olfactory' motor plan is not immediately excluded as the visual target appears (as it can be noticed on the fingers' angular excursion profiles), but penetrates the 'visual' motor plan. Such intrusion results in an on-line adjustment which renders the system more unstable and therefore determines a decrease in the level of covariation amongst digits. In line with the hypothesis that dealing with the intrusion of a 'large' odour is easier than dealing with the intrusion of a 'small' odour, the temporal window in which the decrease in the level of covariation was found it was greater when the olfactory stimulus was 'small' and the visual target was 'large' than when the olfactory stimulus was ‘large’ and the visual target was ‘small’.

3.4.2 When the olfactory ‘size’ do match the visual ‘size’ facilitation emerges

When a preceding odour elicits a ‘grasp’ plan which is congruent with the ‘grasp’ plan subsequently established for the visual target, the kinematic patterning is magnified. Therefore, the grasp plan triggered by the olfactory stimulus primed the grasp plan established for the visual target. This effect was evident at the very beginning of the movement, fading away during the second phase of the movement. Remember that for both the incongruent conditions (i.e., SL and LS conditions) the conflict between the ‘olfactory’ and the ‘visual’ grasp plans lasted for the entire movement duration. Importantly, and again in contrast with what reported for the incongruent conditions, an odour of a similar ‘size’ than the visual target, does not alter hand synergies with respect to when no odour is presented. This indicates that when the ‘size’ of the odour and the size of the visual target match, the integration of the two modalities reinforces the ‘grasp’ plan, the established synergic pattern is more ‘protected’ and it does not change. Having two sources carrying similar information leads to a more stable and coherent action.

Research on multisensory processing brings evidence of enhancements of multimodal neurons’ firings, perceptual processes, or reaction times, in response to stimuli with similar characteristics represented in different modalities (Stein & Meredith, 1990; Rolls &

Baylis, 1994; Stein, Wallace, & Meredith, 1995; Giard & Peronnet, 1999; Calvert, 2001). More recently, similar enhancements have also been found for prehensile tasks (Patchay et al. 2003; Patchay et al., 2006; Zahariev & MacKenzie, 2007). For instance, reach-to-grasp movements were faster if two cues related to the same target object pertained to different sensory modalities, i.e., visual and auditory than when only one cue is presented (Zahariev & MacKenzie, 2007). The present results crucially extend this literature by demonstrating that similar facilitation effect can also be revealed for multisensory integrations involving olfaction.

4. Effects of olfactory stimuli on arm-reaching duration[4]

Abstract

The aim of the present study was to investigate the effects of olfactory stimuli on visually guided reaching. In Experiment 1, participants reached towards and grasped either a small (almond/strawberry) or a large (apple/orange) visual target. One of four odours corresponding to the visual stimuli or odourless air was administered before movement initiation. Within the same block of trials, participants smelled (*i*) an odour associated with an object of a different size than the target, (*ii*) an odour associated with an object of a size equal to that of the target, or (*iii*) odourless air. Results indicated that reaching duration was longer for trials in which the odour 'size' and the visual target-object did not match than when they matched. In Experiment 2, the same procedures were applied but the 'no-odour' trials were administered in a separate block to the 'odour' trials. Similar results as for Experiment 1 were found. However, in contrast to Experiment 1, the presence of an odour increased the level of alertness resulting in a shortening of reaching duration. We contend that olfactory stimuli have the capacity to elicit motor plans interfering with those programmed for a movement toward a visual target-object.

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[4] *Published*: Tubaldi, F., Ansuini, C., Demattè, M.L., Tirindelli, R., & Castiello U. (2008). Effects of olfactory stimuli on arm reaching duration. *Chemical Senses*, *33*, 433-440.

4.1 INTRODUCTION

As shown in the previous chapter the effects of multisensory coding during a natural grasping task have been extended to the chemosensory modalities (Castiello et al., 2006; Tubaldi et al., 2008a). It was demonstrated that odour information can modulate a complex motor system such as that subtending hand grasping. When participants smelled an odour associated with a large fruit prior to grasping a small fruit, a pattern of hand aperture more related to a grasp for a large fruit than to a grasp for a small fruit was found. Conversely, when participants smelled an odour associated with a small fruit before grasping a large fruit, a pattern of hand aperture more related to grasping for a small fruit than to grasping for a large fruit was found (Castiello et al., 2006; Tubaldi et al., 2008a). In other words, hand aperture for the action toward the target was scaled with respect to the size of the object associated with the olfactory stimulus.

Here, we capitalize on these latter findings (Castiello et al., 2006; Tubaldi et al., 2008a) to address the following questions. First, whether it is not only the grasp component but also the reaching component that is modulated by the size of the object associated with the olfactory stimulus. In this respect, previous reach-to-grasp literature has demonstrated that both the grasp and the reaching components are influenced by the size of the visual object (Gentilucci et al., 1991; Jakobson & Goodale, 1991). Specifically, reaching duration increases for reach-to-grasp movements directed toward smaller compared with larger objects (Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Gentilucci et al., 1991; Jakobson & Goodale, 1991). Furthermore, remember that when reaching toward and grasping a smaller target in the presence of a larger distractor reaching duration decreases, whereas it increases in the opposite combination (e.g., Castiello, 1996). Therefore, if reaching duration for a small target decreases in the presence of a 'large' than a 'small' odour and increases for movements toward a large target in the presence of a 'small' than a 'large' odour, then inference regarding the influence of odour 'size' on reaching temporal organization may be advanced.

The second question concerns possible facilitation effects on reach duration depending on the increase in alertness triggered by the delivery of any odour regardless of its 'size'. In this respect, previous evidence indicates that the delivery of visual and auditory cues before and during movement determines faster reach-to-grasp movements (Castiello, 1999; Zahariev & MacKenzie 2007). Therefore, it might well be that olfactory cues also determine a level of alertness which manifests in a shorter reaching duration. This assumption finds some support from previous olfactory research suggesting that the presence of odours increases alertness in various tasks (Warm, Dember, & Parasuraman, 1991; Dember, Warm, & Parasuraman, 1995; Millot, Brand, & Morand, 2002). As an example, Millot et al. (2002) reported that simple reaction times to visual and auditory stimuli were accelerated by the presence of ambient odours regardless of their pleasantness. Therefore, if the presence of olfactory information determines a generalized facilitation effect, then such facilitation might also be evident in reaching duration.

4.2 METHODS

4.2.1 Participants

Twenty-six right-handed subjects (13 females and 13 males, mean age = 22 years, standard error of the mean [SEM] = 3.5 years) took part in the Experiment 1. Twenty-three right-handed subjects (12 females and 11 males, mean age = 22 years, SEM = 2 years) took part in the Experiment 2. Both experimental sessions lasted approximately 30 min.

4.2.2 Procedures

The task for participants was to reach, grasp and lift a visual target-object either in the absence or in the presence of a nontarget olfactory stimulus (see Chapter 2). This task could be performed under six different experimental conditions: OL, OS, LL, SS, SL, LS conditions (see Chapter 3).

In Experiment 1 participants performed a block of 48 trials (8 for each experimental condition) within which trials for all experimental conditions were presented in a fully randomized order. For Experiment 2, 48 trials were included in 2 different blocks: 'No odour' and 'Odour' blocks. For the 'No odour' block, a total of 16 trials was administered, 8 for the OL condition and 8 for the OS condition. For the 'Odour' block a total of 32 trials was administered, 8 trials for each odour ‘size’/target size combination (i.e., SS, LL, SL, and LS condition). Within both the ‘No odour’ and ‘Odour’ blocks, the trials were presented in a randomized order. The order of block presentation was strictly alternated across participants. In order to avoid possible between-block carry-over effects, an inter-block interval of 2 minutes was administered.

4.2.3 Stimuli and apparatus

Stimuli and apparatus adopted in the present experiment have been described within the ‘General methods’ section (see Chapter 2).

4.2.4 Data analysis

In order to asses the experimental hypotheses, we first tested whether reaching duration was shorter when the to-be-grasped object was large than when it was small (contrast vector: [OL + LL + SL] > [OS + SS + LS], see Chapter 2). Then, we ascertained whether reaching duration was: (*i*) longer for a large target when the delivered odour was associated with a small object than when it was associated with a large object (contrast vector: SL > LL condition, see Chapter 2); (*ii*) shorter for a small target when the delivered odour was associated with a large object than when it was associated with a small object (contrast vector: LS < SS condition, see Chapter 2). Finally, we evaluated whether reaching duration was (*iii*) shorter when an odour was delivered than when no odour was presented (contrast vector: [SL + LL + LS + SS]/4 < [OS + OL]/2, see Chapter 2). We used one-tailed t-tests since the aforementioned effects had a specific direction (see Chapter 2).

4.3 RESULTS

This section will be organized in two parts. One for each of the two Experiments.

4.3.1 Experiment 1

The analyses revealed that reaching duration was shorter when the object to be grasped was large than when it was small (Large = 1268 ± 70 ms; Small = 1348 ± 65 ms, $t_{25} = 6.01$, $P < 0.001$; see Figure 4.3.1.1). Further, reaching duration was longer for the SL (red bar) than for the LL (blue bar) condition (SL = 1276 ± 70 ms; LL = 1255 ± 69 ms, $t_{25} = 1.70$, $P < 0.05$; see Figure 4.3.1.1). In contrast, reaching duration was not significantly different for the LS (green bar) and the SS (purple bar) condition (LS = 1352 ± 64 ms; SS = 1334 ± 67 ms, $t_{25} = 1.16$, $P > 0.05$; see Figure 4.3.1.1). Finally, no significant differences were found when comparing reaching duration for trials in which odourless air was delivered with reaching duration for trials in which an odour was presented (No odour = 1314 ± 70 ms; Odour = 1305 ± 67 ms, $t_{25} = 0.67$, $P > 0.05$).

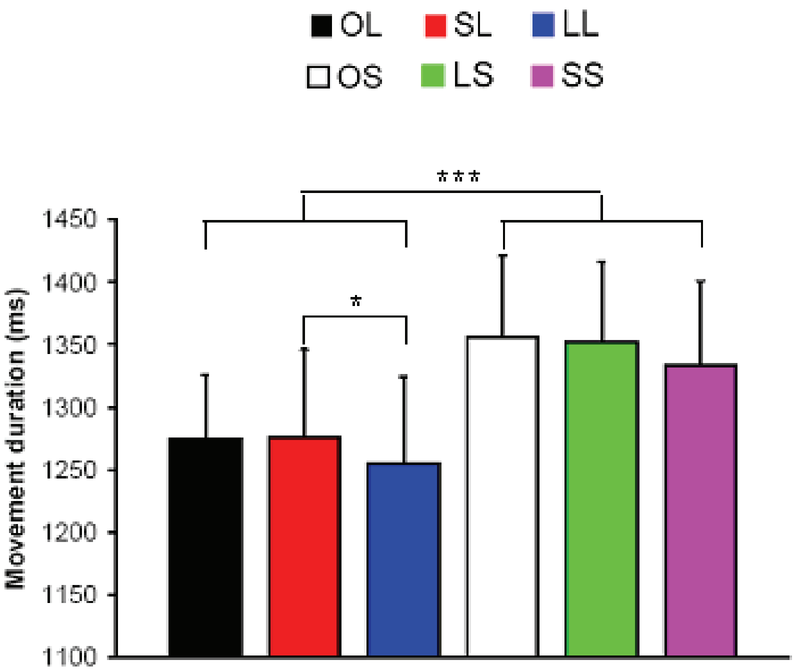

Figure 4.3.1.1 Mean movement duration for OL (Odourless air-Large target), SL (Small odour-Large target), LL (Large odour-Large target), OS (Odourless air-Small target), LS (Large odour-Small target), and SS (Small odour-Small target) conditions for Experiment 1. Error bars indicate SEM. Asterisks indicate significant values (***$P < 0.001$; *$P < 0.05$).

4.3.2 Experiment 2

The analyses revealed that reaching duration was shorter when the to-be-grasped object was large than when it was small (Large = 1514 ± 70 ms; Small = 1597 ± 73 ms, $t_{22} = 5.90$, $P < 0.001$) (see Figure 4.3.2.1, top panel). As depicted in Figure 4.3.2.1 (top panel), reaching duration was longer for the SL (red bar) than for the LL condition (blue bar) (SL = 1504 ± 90 ms; LL = 1469 ± 83 ms, $t_{22} = 2.98$, $P < 0.01$). Similarly, reaching duration for the LS condition (green bar) was longer than for the SS condition (purple bar) (LS = 1575 ± 84 ms; SS = 1544 ± 84 ms, $t_{22} = 2.36$, $P < 0.05$) (see Figure 4.3.2.1, top panel).

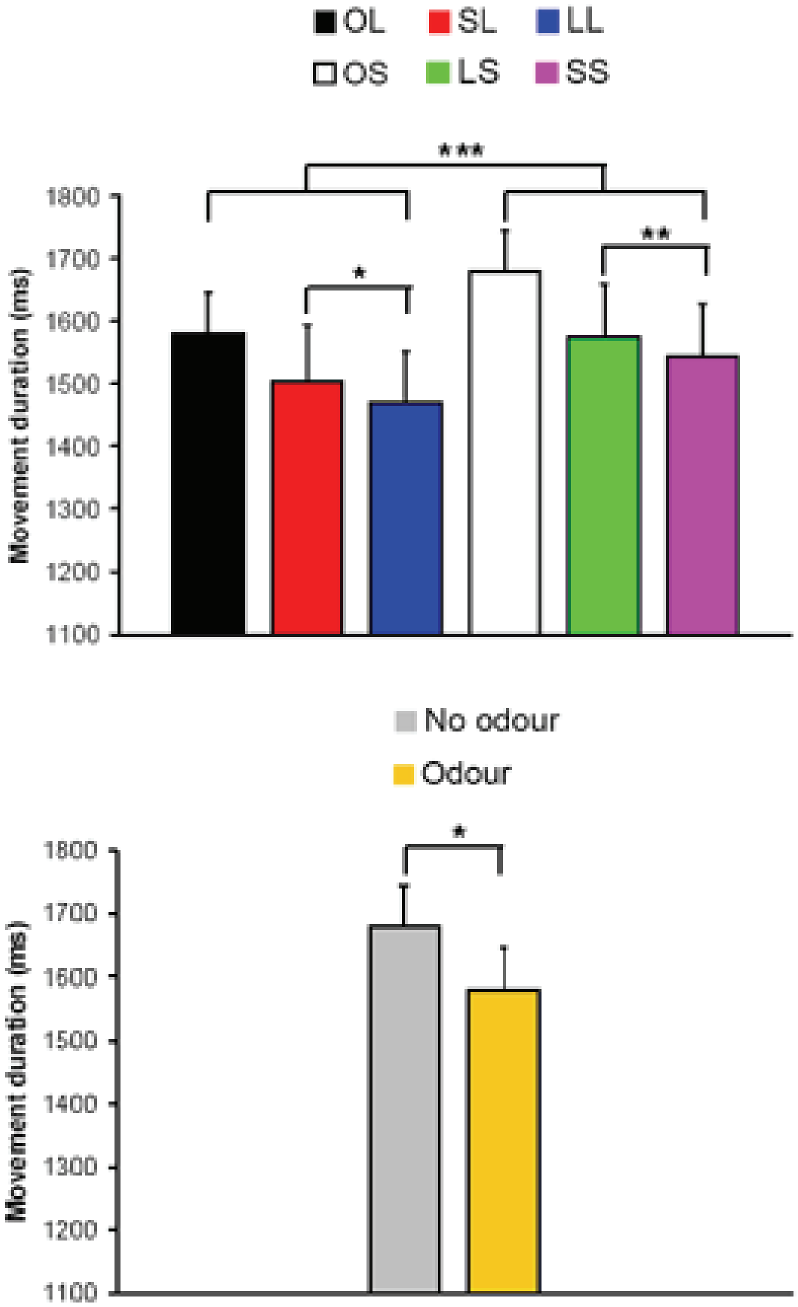

Figure 4.3.2.1 Mean movement duration for the OL (Odourless air-Large target), the SL (Small odour-Large target), the LL (Large odour-Large target), the OS (Odourless air-Small target), the LS (Large odour-Small target), and the SS (Small odour-Small target) conditions for Experiment 2 (top panel). Mean movement duration for the 'No-odour' (odourless air delivered before reaching for the target) and the 'Odour' (either 'small' or 'large' odour administered before reaching for the target) blocks for Experiment 2 (bottom panel). Error bars indicate SEM. Asterisks indicate significant values. (Upper panel: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; lower panel: * $P < 0.05$).

In general, these findings replicated those for Experiment 1. Further, as reported in Figure 4.3.2.1 (bottom panel), reaching duration was longer for trials in which odourless air was delivered (i.e., gray bar) with respect to trials in which an odour was administered (yellow bar) (No odour = 1621 ± 58 ms; Odour = 1523 ± 85 ms, $t_{22} = 1.83$, $P < 0.05$).

4.4 DISCUSSION

We set out to investigate the effect of olfactory information on the duration of a reaching movement toward a visual target. The results indicate that reach duration was affected by the delivery of an olfactory stimulus when the size of the object associated with the odour was different from the size of the visual target. Furthermore, when trials preceded by the delivery of an odour were administered separately from trials in which the odour was not delivered, the presence of an olfactory stimulus determined a facilitation effect, which was evident as a shortening in reaching duration.

4.4.1 The effect of odour 'size' on reaching duration

In the present study, when the odour was associated with an object of a different size than the visual target, reaching duration increases. This finding partially confirms our hypotheses concerned with an effect of olfactory information, in terms of 'size', on reaching duration. In line with our prediction, reaching duration is longer for a movement toward a large target following the delivery of a 'small' odour than following the delivery of a 'large' odour. However, in contrast to our prediction, reaching duration does not decrease for a movement toward a small target following the delivery of a ‘large’ odour in comparison to a similar kind of action performed following the delivery of a ‘small’ odour. Indeed, the delivery of a ‘large’ odour determined an increase rather than a decrease in reaching duration as our hypothesis would predict.

We suspect that it is the relationship between the motor representations elicited by the ‘small’ and the ‘large’ odours and the accuracy requirements dictated by the visual target, which may account for such a difference. To elaborate, the ‘grasp’ plan elicited by the ‘small’ odour calls for a precise positioning of fingers upon the target object (i.e., PG). Therefore, such an accurate demand might be responsible for the increase in reaching duration for movements performed toward the large visual target in the presence of a ‘small’ odour. Conversely, when the ‘large’ odour is presented, the less accurate demand associated to this ‘grasp’ plan (i.e., WHG) might not be suitable to grasp a small visual target-object requiring a greater level of accuracy. In this respect, a relevant issue to consider is the level of coordination between the reaching and the grasping components during prehension (e.g., Jeannerod, 1981). In particular, the reaching component subserves the grasping component by adapting its duration to the end goal accuracy requests. In this view, the fact that when the ‘large’ odour was presented it did not elicit a faster movement toward a small visual target makes some sense. This is because a fast movement would have prevented the accomplishment of the accuracy demands characterizing a precise grasp toward the small visual target. That is, the selection of specific fingers (i.e., index finger and thumb) and contact points (e.g., Gentilucci et al., 1991). Conversely, adding accuracy (i.e., 'small' odour) to a movement directed toward a large visual target-object would not dramatically prevent the completion of a successful action.

It is now necessary to comment on the mechanisms through which the size information conveyed by the odour affects reaching for a visual target. In this respect, the motor system is particularly efficient in managing the relationships between sensory and motor variables in order to achieve the action end goals. To do this, it converts quickly and effortlessly the features of an object into motor commands forwarded to the effectors moving toward that object (Castiello, 1999) and simultaneously predicts the outcome for this motor plan (Jordan & Wolpert, 1999). When a change in object features occurs, the initial motor plan might be no longer suitable for the new end goal. Under these circumstances, the motor system may predict such a discrepancy and retunes the old motor plan according to requirements imposed by the new end goal features (Kawato, 1999). A substantial body of work has demonstrated that these dynamic mechanisms are put in place when objects' features are encoded within the same sensory domain, that is, visual (Castiello, 1999; Wolpert & Ghahramani, 2000). Similar mechanisms, however, may also explain the present 'multisensory' findings. When the accuracy demands dictated by the action end goal are satisfied by the reach duration established for the object associated with the odour, the motor plan elicited by the olfactory information does not need to be changed; as it happens when the odour is ‘small’ and the visual stimulus is large. Conversely, when reach duration established according to the odour cannot satisfy the prerequisites for acting successfully upon the visual target, a correction is applied; as it happens when the odour is ‘large’ and the visual target is small. This correction would be played out on a longer reach duration.

4.4.2 The presence of the odour alerts reaching actions

In Experiment 1, no significant differences were found when comparing trials in which the odour was present with trials in which the odour was absent. This finding did not confirm the hypothesis that odours may increase the level of alertness, thus determining a faster reaching movement. However, we suspect that this lack of effect could be ascribed to the fact that the ‘odour’ and the ‘no odour’ trials were intermingled within the same block. This is because the level of alertness reached during ‘odour’ trials (i.e., LL, SS, SL, and LS condition) may carry over into ‘no-odour’ trials (i.e., OL and OS condition), rendering undetectable the net effect. In order to rule out the possibility that in the Experiment 1 facilitation effects were masked by the concurrent presentation of different types of trial within the same block, we performed Experiment 2. Experiment 2 was similar in all aspects to Experiment 1 except that participants performed the ‘odour’ and the ‘no-odour’ trials in separate blocks. Administration of trials in separate blocks would prevent carry over effect and, in turn, the alertness effect should emerge. As expected, results from the Experiment 2 showed that the mere presence of an odour produced a generalized decrease in reaching duration.

Alertness in behavioural terms ranges from sleep to wakefulness and may be defined experimentally in terms of speed of information processing. When considering previous literature, it emerges that enhancements in alertness dictated by olfactory stimuli have been chiefly investigated by means of simple sensory-motor tasks requiring participants to perform arbitrary responses such as reaction time (Millot et al., 2002; Barker et al., 2003). As an example, Millot et al. (2002) found that reaction time in simple tasks (responses to visual or auditory stimulation) significantly decreased in ambient odour conditions compared to no-odour condition. Thus, the reported facilitation effect on movement duration - due to olfactory stimulation regardless of odour size - can be considered as a new piece in the puzzle of odour-induced behaviour. This result may signify that an odour stimulus works as a cue which increases the level of alertness not only in terms of action initiation but also in terms of action execution. Further, the present findings add to a growing body of literature which is starting to reveal the nature of multisensory mechanisms underlying reach-to-grasp movements (Castiello, Badcock, & Bennett, 1999; Patchay et al., 2003; Patchay et al., 2006; Castiello et al., 2006; Zahariev & MacKenzie, 2007; Castiello et al., 2007; Tubaldi et al., 2008a). For instance, faster movement times have been found when redundant auditory information was presented (Zahariev & MacKenzie, 2007). Therefore, the presence of auditory cues was able to increase the level of alertness during action execution. In this perspective, it might well be that olfactory information as any other modality has the potential to increase the level of alertness during an overt action.

5. Differential effects of task-irrelevant olfactory information on the planning and the execution of reach-to-grasp movements[5]

Abstract

Previous evidence indicates that, when reaching to grasp a visual target, the presence of distractors presented either in the visual or olfactory modality determines significant interference effects. However, whereas research on visual distractors has also revealed that such interference effects disappear when prior knowledge about the target is given to participants, this aspect for olfactory distractors has yet to be investigated. Therefore, here we asked participants to reach towards and grasp a small or a large visual target following the delivery of an odour evoking either a small or a large object. When the type of grasp evoked by the odour did not coincide with that for the visual target, interference effects were evident on reach duration and reaction time, but kinematics of hand shaping remained unaltered. This study demonstrates that, when participants knew in advance which object was the target, olfactory distractors produced no interference effects on movement kinematics, but they did on key temporal measures, i.e., reaction time and reach duration.

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[5] *Published*: Tubaldi, F., Ansuini, C., Tirindelli, R., & Castiello, U. (2009). The effects of task-irrelevant olfactory information on the planning and the execution of reach-to-grasp movements. *Chemosensory perception*, *2*, 25-31.

5.1 INTRODUCTION

The evidence so far reported in the present thesis suggests that olfaction, as other sensory modalities, has the ability to convey information which is relevant for interacting with objects (e.g., shape, size; Castiello et al., 2006; Tubaldi et al., 2008a; Tubaldi, Ansuini, Demattè, Tirindelli, & Castiello, 2008b).

Here, we wanted to investigate whether the reported interfering effects fades away when the participants know in advance the nature of the visual target. This is an important aspect to consider because previous research considering distractor presented in other modalities reported that if participants had previous knowledge regarding the target then interference effects were not evident (Castiello, 1996; Jackson et al., 1995; Tipper et al., 1997). In other words, given sufficient time to select the more appropriate visuomotor representations as to guide the hand to the target, and to inhibit successfully those of the competing nontarget, significant interference effects disappear.

We reasoned that if previous knowledge of the visual target allows for an efficient filtering of non-target olfactory information, then no effects on movement kinematics and movement duration should be evident. However, we expect that traces of such filtering might be present on temporal measures that reflect the processes underlying movement planning, i.e., reaction time. In contrast, if interference effects still persist in such conditions, then speculations regarding possible differences in the filtering of irrelevant information depending on sensory modality might be advanced.

5.2 METHODS

5.2.1 Participants

Nine right-handed participants (four females; mean age = 21 ±standard error [SEM] =2 years) took part in the experiment. The experimental session lasted approximately 30 min.

5.2.2 Procedures

The task for participants was exactly the same as for the previous experiment except that participants initiated the movement following the presentation of the visual target. Specifically, the sequence of events for each trial was as follows: (*i*) vision was occluded before the target was positioned on the working surface; (*ii*) an auditory tone (850 ms duration, 65 dB sound pressure, and 800 Hz frequency) indicated odour delivery; (*iii*) after 3 s, a similar tone indicated the offset of odour delivery; (*iv*) the lenses of the spectacles were cleared. Following this event, participants decided when to start the action.

For the present investigation, in addition to kinematics and movement duration (see Chapter 2), reaction time was also recorded. This latter variable was calculated as the time interval between the opening of the spectacles and the time at which the starting switch was released (see Chapter 2).

5.2.3 Stimuli and apparatus

Stimuli and apparatus adopted in the present experiment have been described within the 'General methods' section (see Chapter 2).

5.2.4 Data analysis

To assess how the experimental conditions affected both movement duration and reaction time, two analyses of variance (ANOVAs) with odour size ('large', 'small') and target size (large, small) as within-subjects factors were performed (see Chapter 2). Results from ANOVAs were explored by means of pair-wise comparisons (see Chapter 2). The effect of the experimental conditions on hand shaping was tested entering angular excursion for all digits' joints and distances into an ANOVA with odour size ('large', 'small'), target size (large, small), and time (from 10 to 100%, by step of 10%) as within-subjects factors (see Chapter 2).

5.3 RESULTS

The interaction odour size by target size was significant for both movement duration [$F_{(1,\ 8)} = 11.76$, $P < 0.001$] and reaction time [$F_{(1,\ 8)} = 7.25$, $P < 0.05$]. For movement duration, when the target was large, post hoc analyses revealed that movement duration was longer when the 'size' of the odour did not match the size of the target (i.e., SL condition) with respect to when the two 'sizes' did match (i.e., LL condition) [M = 1559 ms; SEM = 119 ms *vs.* M = 1495 ms; SEM = 119 ms, respectively, $t_{(8)} = 3.05$, $P < 0.05$, see Figure 5.3.1a]. In contrast, when the target was small, pair-wise comparisons showed that movement duration for the LS condition was similar to that observed for the SS condition [M = 1547 ms; SEM = 119 ms *vs.* M = 1510 ms; SEM = 108 ms, respectively, $t_{(8)} = 2.10$, $P > 0.05$, see Figure 5.3.1a]. For reaction time, when the target was large, there were no significant differences when comparing the SL with the LL condition [M = 540 ms; SEM = 67 ms vs. M = 537 ms; SEM = 54 ms, respectively, $t_{(8)} = 0.01$, $p > 0.05$, see Figure 5.3.1b]. Conversely, for a small target, reaction time was longer when the ‘size’ of the odour did not match the size of the target (i.e., LS condition) with respect to when the two ‘sizes’ did match (i.e., SS condition) [M = 592 ms; SEM = 72 ms vs. M = 516 ms; SEM = 64 ms, respectively, $t_{(8)} = 2.40$, $P < 0.05$, see Figure 5.3.1b]. With respect to measures related to hand shaping, when the target was large and the odour was associated with a small object (i.e., SL condition), only the ring-little angular distance showed over-adduction than when an odour associated with a large object was delivered (i.e., LL condition) [interaction: odour size by target size, $F_{(1,\ 8)} = 10.95$, $P < 0.01$, see Figure 5.3.2a]. This effect was particularly evident within the second half of movement duration (i.e., from 50% up to 100% of normalized reach duration) [interaction: odour size by time, $F_{(2.06,\ 16.49)} = 3.42$, $P = 0.056$, see Figure 5.3.2a]. When the target was small, the mismatch between the ‘size’ of the odour and the size of the visual target did not significantly affect angular excursion for all digits’ joints and distances ($P_s > 0.05$; for an example, see Figure 5.3.2b).

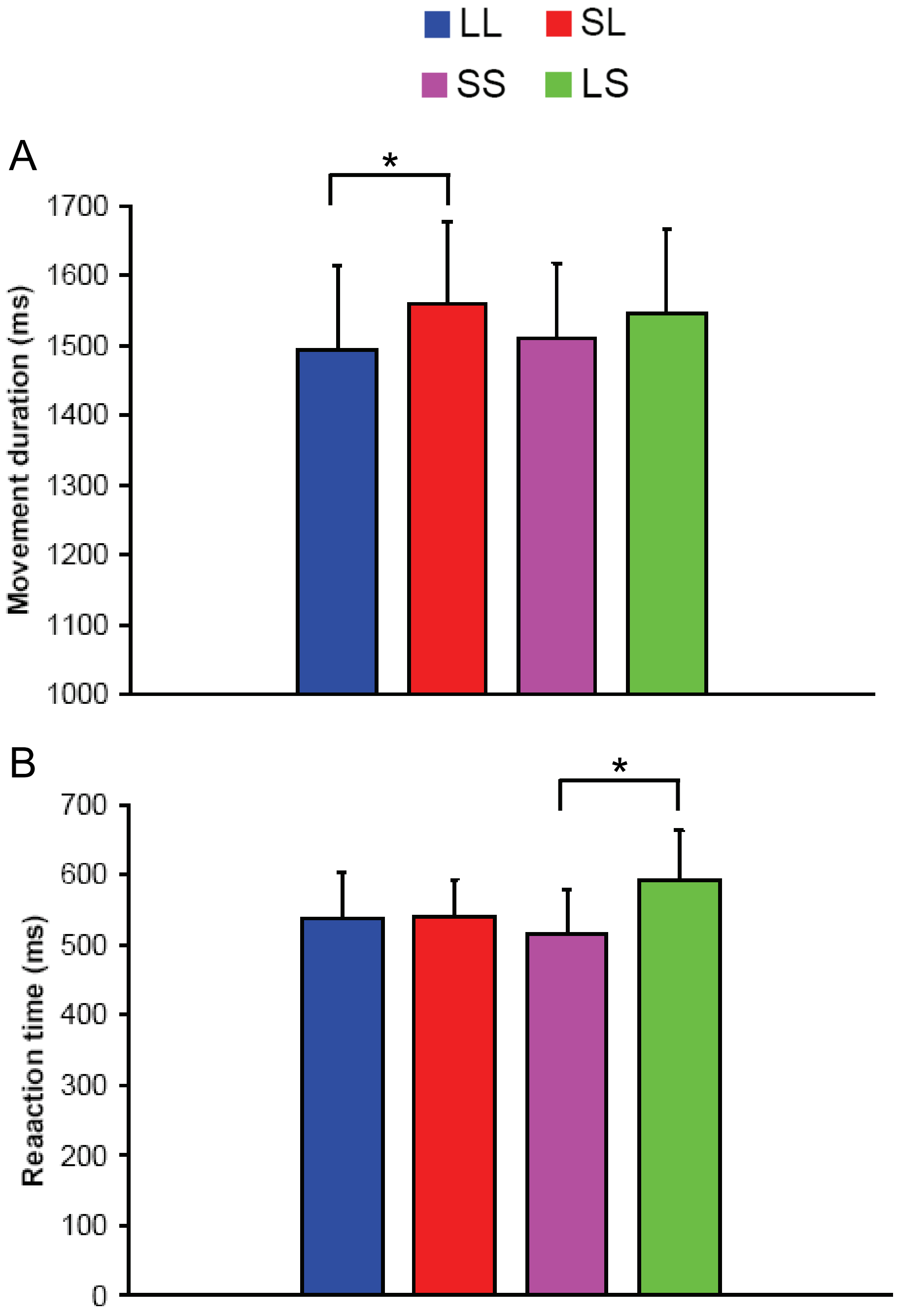

Figure 5.3.1 Mean movement duration (A) and mean reaction time (B) for each odour 'size'/visual target size combination, i.e., Large odour-Large target (LL), Small odour-Large target (SL), Small odour-Small target (SS), and Large odour-Small target (LS). Error bars indicate SEM. Asterisks indicate significant values ($P < 0.05$)

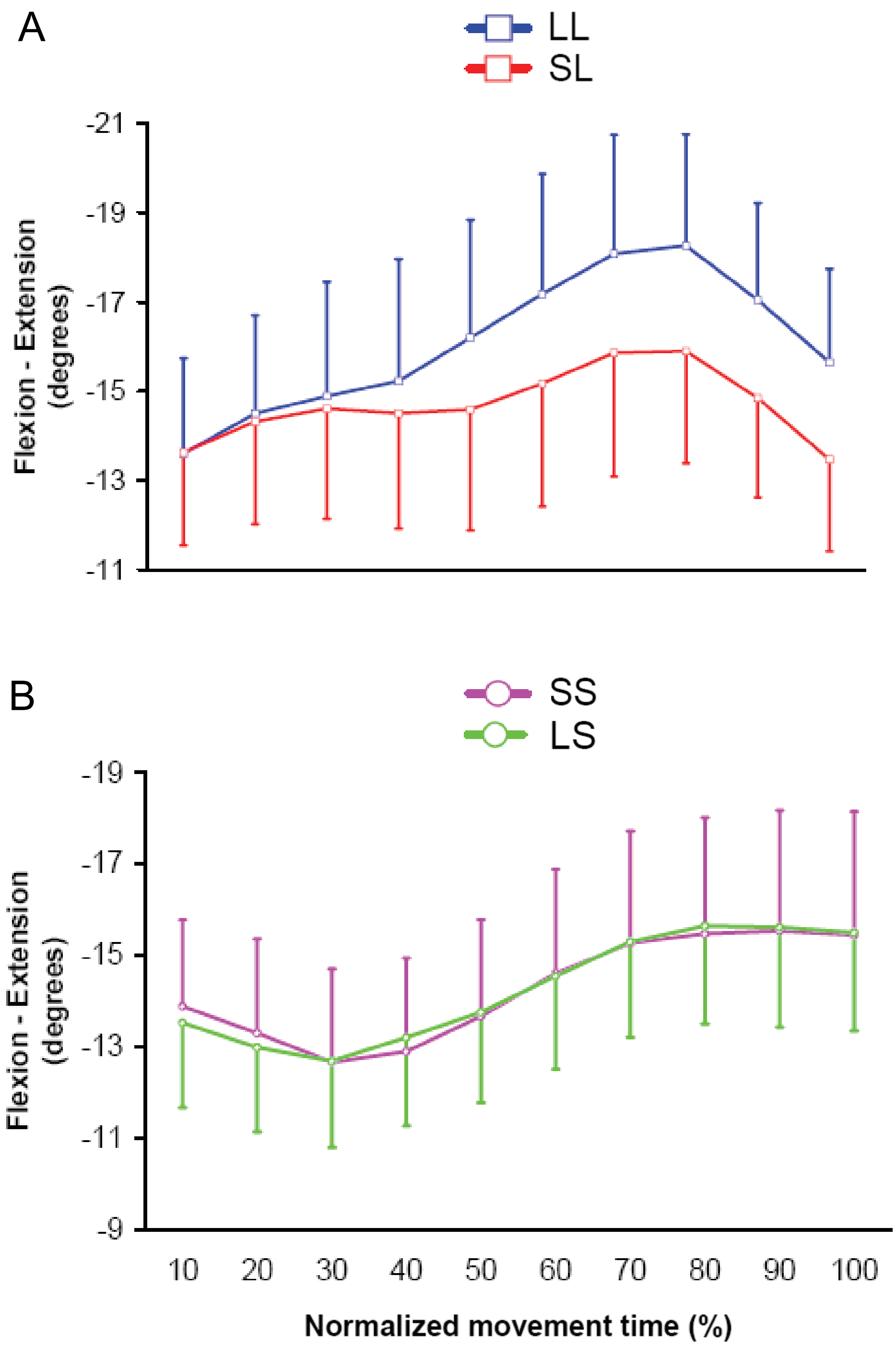

Figure 5.3.2 Time course of angular distance between the ring and the little fingers. Each trace corresponds to the time course of the average angular distance for (A) the Large Odour-Large Target (LL) condition and the Small odour-Large target (SL) condition and for (B) the Small odour-Small target condition (SS) and the Large odour-Small target condition (LS). Error bars represent SEM.

5.4 DISCUSSION

We set out to investigate whether previous knowledge of the features characterizing a target minimizes the interference effects that nontarget olfactory stimuli might have on the planning and execution of a reach-to-grasp movement. We found two opposite patterns of results for reaction time and movement duration depending on the relationship between the ‘size’ of the odour and the size of the visual target.

When the ‘size’ of the odour was small and the visual target was large, movement duration increased, but reaction time remained unchanged; when the ‘size’ of the odour was large and the visual target was small, reaction time increased, but movement duration was unaltered. Further, effects due to the mismatch between the ‘size’ of the odour and the size of the visual target were evident on a fingers’ distance only when the visual target was large.

Previous research concerning reaching and grasping has shown interference effects of distractors presented in the visual modality disappeared on movement kinematics when they were presented long before overt behaviour began (Castiello, 1996; Chieffi, Gentilucci, Allport, Sasso, & Rizzolatti, 1993; Jackson et al., 1995). Here, we extend this literature by demonstrating that, when nontargets are signalled via olfaction, prior knowledge of a visual target does not completely prevent interference effects from taking place. These findings suggest that the selection process underlying a reach-to-grasp movement acts in a different fashion when either olfactory or visual nontarget information has to be filtered out. In the case of visual nontarget information, participants seem to be able to complete the selection processes before beginning to reach. Thus, on-line selection was not required because sufficient time was available to select the motor representations that guide the hand to the target and to successfully inhibit those of the competing distractor. A possible explanation for the present findings needs a discussion that intermingles the nature of the effects concerned with the used dependent measures. Reaction time is an established indicator of the complexity of movement preparation (Hick, 1952). Digits' distances and movement duration are measures that reflect changes on movement execution when task-irrelevant information is presented (Tipper et al., 1997; Tipper, Lortie, & Baylis, 1992; Meegan & Tipper 1998; Pratt & Abrams, 1994; Ansuini, Tognin, Turella, & Castiello, 2007).

With this in mind, our preferred explanation for the present results is the following: When the delivered odour was 'small' and the visual target was large, participants prepared the movement on the basis of the 'small' odour, thus preparing a motor plan for an object that, in principle, requires a level of accuracy higher than that for a larger object. We suspect that, in such circumstances, reaction time did not increase because the motor plan prepared on the basis of the 'small' odour considered a level of accuracy that could satisfy the grasping of a large object. If this is correct, then off-line corrections, which, in principle, should bring changes in reaction time, might not be needed.

A point to consider, however, is that the motor plan suited to grasp a small object is not suited to grasp a large object in terms of fingers' recruitment. For example, when grasping small objects between the thumb and the index finger, the last three fingers (i.e., middle, ring, and little fingers) are flexed, closed to each other, and tend to contact with the palm of the hand. Whereas, when grasping large objects by opposing the thumb to the forefingers, the last three fingers are extended farer from each other and from the palm of the hand. Therefore, an adjustment might be necessary to revise biomechanical constraints. Indeed, the result for the fingers' distance associated to the Small odour-Large target (SL) condition suggests that such adjustment occurs on-line, inducing the observed increase in movement duration. When the delivered odour was 'large' and the visual target was small, instead, the accuracy requirements might have been insufficient to guarantee grasping for a small object. If this were the case, they need to be revised by the system in order to successfully grasp the small object. We suggest that such revision occurs off-line and is operationalized through the significant increase in reaction time. In such circumstances, the system resolved the mismatch in terms of both accuracy and biomechanics (i.e., fingers' recruitment) before movement initiation.

A theoretical account that may explain the present results rests on the notion of response competition, arguing that both the distractor and the target onsets automatically trigger the planning of movements (Meegan & Tipper 1998, Tipper et al., 1998). The observed distractor interference presumably reflects the need to suppress responses towards the distractor once the distractor-related movement plan has been completed. The present finding may add a further level of complexity to this idea, suggesting that, at least for the processing of non-target olfactory information, accuracy plays an important role in determining the time course of interference.

6. Odours grab his hand but not hers[6]

Abstract

Gender is important for the determination of olfactory abilities. Previous reports on gender differences in human odour perception claimed that the sensitivity and discrimination ability of females for odours is superior to that of males. Evolutionary theories, however, open up the possibility of an interesting dissociation between females and males in terms of odour processing: there is an advantage for women for the perceptual aspects of olfactory stimuli and an advantage for men when translating perceptual olfactory information into action. In line with this hypothesis our observations suggest that encoding odours has the ability to guide the movement of males but not that of females.

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[6] *Published*: Tubaldi, F., Ansuini, C., Tirindelli, R., & Castiello, U. (2008). Odours grab his hand but not hers. *Perception,* 37, 1886-1189.

6.1 INTRODUCTION

The observation of gender differences in relation to olfactory abilities dates back to the end of the nineteenth century when Toulouse & Vaschide (1899) claimed that females' sensitivity and discrimination ability for odours is superior to those of males. Their claim was based on the results of a study in which camphor and floral odours were administered to 237 subjects of both sexes and all ages. The notion of female superiority in olfactory perception also appears to be a universal belief, as demonstrated by the outcome of a large survey involving 1.5 million people performed by Wysocki & Gilbert (1989) in collaboration with the National Geographic Society. They found that women had a higher opinion of their olfactory abilities than men independently of their age. In recent years the question of gender differences in chemosensory perception has received increased attention with a variety of psychophysical studies demonstrating that odour perception differs between sexes and this difference still appears to be always in favour of women (Brand & Millot, 2001).

Further support for a female advantage in odour perception comes from the documentation of sexual differences concerning both physiology and morphology of the main olfactory cerebral regions. When odours are presented to subjects as stimulants for functional magnetic resonance imaging, the volume of activated foci in females is eight times bigger than in males (Yousem et al., 1999). Similarly, women express larger amplitudes of event-related potentials on the left hemisphere than men during odorant delivery (Lundström & Hummel, 2006), and concentration of grey matter within specific olfactory areas appears to be higher for females than males (Garcia-Falgueas et al., 2006). Among the theories offered to explain how a female advantage in olfactory perception might have arisen, those relying on an evolutionary perspective are particularly gripping (Velle, 1987). It has been proposed that sex differences have been selected to compensate for the weaker physical strength of women. In this perspective women might have shown less effective defensive aptitudes than men. This might have brought to an early division of labour with the main task for women to gather food supply which were essentially of plant origin. Therefore, women might have developed superiority in olfaction and taste to distinguish toxic from non-toxic plants and possibly for the evaluation of their nutritional value (Velle, 1987).

Evolutionary theories, however, also reported sex differences in sensory processing which speak in favour of men and might have implications for olfactory processing. According to the 'Man Hunter' and the 'Man Sexual Competitor' models, the males' participation in archaic activities, such as those sub-serving plundering and sexual competing behaviour, has produced an actual advantage in managing the geometry and dynamics for acting on 3-D visual objects (Ecuyer-Dab & Robert, 2004). We found the assumptions behind these theories interesting, because, if men had extended the action-tailored functioning of perception from visual to olfactory domain, then these assumptions would allow us to predict the possibility of gender dissociation in terms of task-related olfactory processing. Whereas female advantage in extracting relevant properties of olfactory stimuli might be confined to purely perceptual aspects, men might be better than women when the situation implies the translation of olfactory information into action.

To test this we compared the performance of males and females participants when performing a task similar to the task adopted in the experiments reported above. If males are more sensitive than women when processing olfactory information within an ‘action’ context, then the olfactory-related motor effects previously reported should be more pronounced for males than females.

6.2 METHODS

6.2.1 Participants

Twenty participants (10 females; mean age = 10 years, SEM = 2 years) took part in the experiment. The experimental sessions lasted approximately 30 min.

6.2.2 Procedures

The task for participants was exactly the same as the task used for the experiment described in Chapter 3 (see also Chapter 2).

6.2.3 Stimuli and apparatus

Stimuli and apparatus adopted in the present experiment have been described within the ‘General methods’ section (see Chapter 2).

6.2.4 Data analysis

To assess how the gender did affect movement duration for the incongruent than for the congruent conditions, movement duration was entered into a three-way ANOVA with gender (male, female) as between-subject factor, odour size ('large', 'small') and target size (large, small) as within-subject factors (see Chapter 2). Then, results from the ANOVA were explored by means of pair-wise comparisons (see Chapter 2).

6.3 RESULTS

Gender did affect the increase in movement duration found for the incongruent than for the congruent conditions [three-way interaction: $F_{(1, 18)} = 4.54$, $P < 0.05$]. For men, movement duration was longer for both the SL than for the LL condition [M = 1625; SEM = 146 ms vs. M = 1568 ms; SEM = 137 ms), $t_{(9)} = 4.10$, $P < 0.01$, see Figure 6.3.1a] and for the LS than for the SS condition [M = 1724 ms, SEM = 145 ms vs. M = 1663 ms, SEM = 146 ms, $t_{(9)} = 2.95$, $P < 0.05$, see Figure. 6.3.1b]. For women, movement duration was not affected by the mismatch between the 'size' of the odour and the size of the visual target (all *Ps* > 0.05, see Figure 6.3.1a-b).

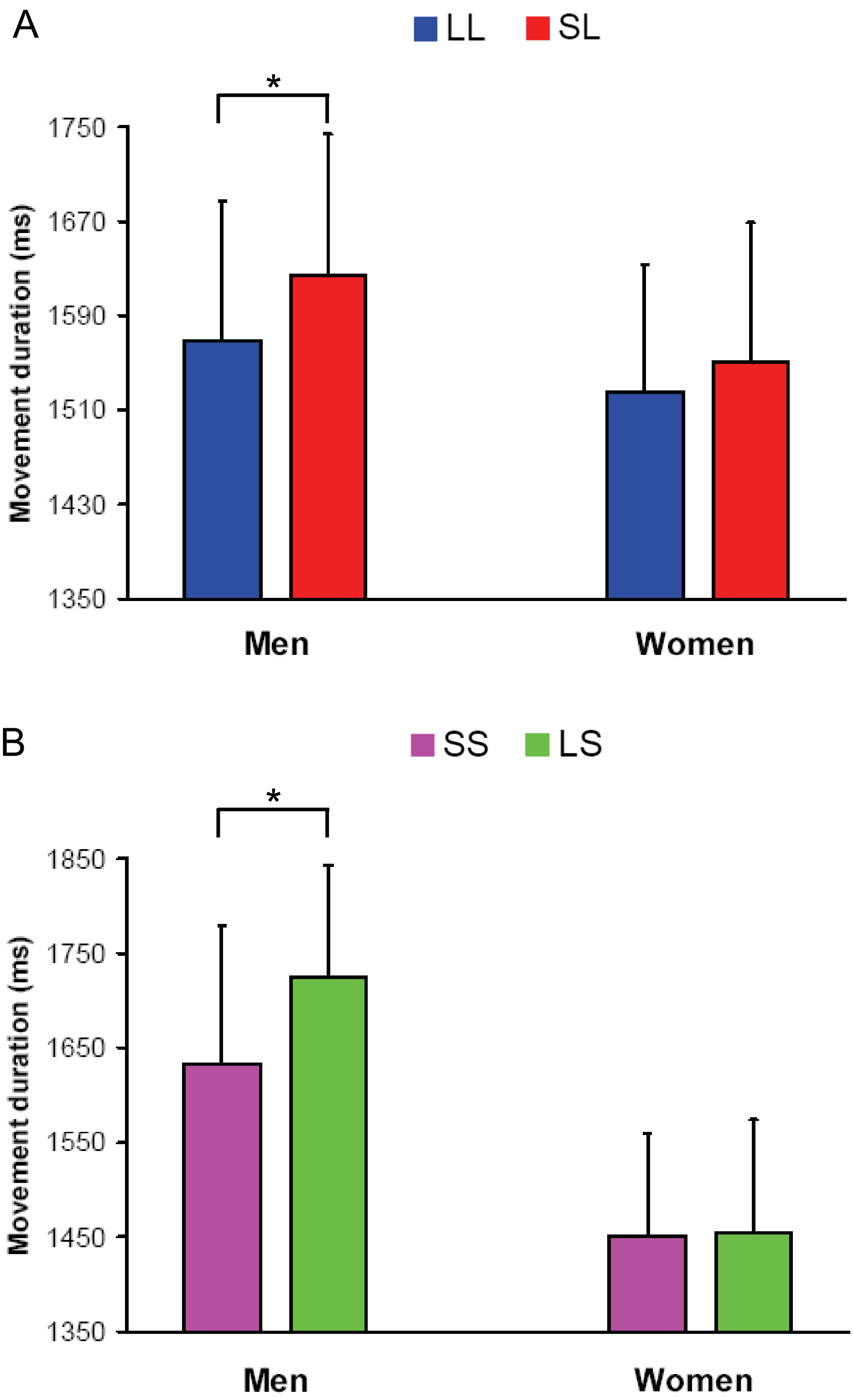

Figure 6.3.1 The gender-differentiated effect of odour on movement duration. Panel A refers to the condition in which either men or women grasped a large target in the presence of an odour associated with an object either smaller or of the same size as the target-object (i.e., SL and LL condition, respectively). Panel B refers to the condition in which either men or women grasped a small target in the presence of an odour associated with an object either larger or of the same size as the target-object (i.e., LS and SS condition, respectively). Asterisks indicate significant differences (*$P < 0.05$).

6.4 DISCUSSION

This observation opens up a novel perspective on sex-differentiated olfactory abilities. Whereas previous literature suggests that women 'know' odours better than men, the present results suggest that men may 'act' on odours better than women. In other words, female sense of smell would be perception-oriented, i.e., optimised to detect, discriminate, identify, recognise, and categorise odours (e.g., Brand & Millot, 2001). Conversely, male sense of smell would appear to be action-oriented, i.e., tailored to elicit specific and selective motor commands for interacting with 'smelled-objects'. In this view, gender differences should not be considered in terms of irrevocable, pervasive differences in the brain of two sexes, but as the flip of a switch between male and female behavioural repertoires for which plays a fundamental role the to-be-accomplished environmental requirements.

These observations may provide interesting insights into the mechanisms underlying sensory processing. For instance, exploring such differences might be useful in revealing the possibility that the perception and perception-for-action dissociation previously described for other modalities (e.g., vision; Goodale & Milner, 1991) might be extended to olfaction.

7. Smelling odours, understanding actions[7]

Abstract

Previous evidence indicates that we understand others' actions not only by perceiving their visual features but also by their sound. This raises the possibility that brain regions responsible for action understanding respond to cues coming from different sensory modalities. Yet no studies, to date, have examined if this extends to olfaction. Here we addressed this issue by using functional magnetic resonance imaging (fMRI). We searched for brain activity related to the observation of an action executed towards an object which was smelled rather than seen. The results show that temporal, parietal and frontal areas were activated when individuals observed a hand grasping a smelled object. This activity differed from that evoked during the observation of a mimed grasp. Furthermore, subadditive activity was revealed when the action target-object was both seen and smelled. Altogether these findings indicate the influence of olfaction upon action understanding and its contribution to multimodal action representations.

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[7] *Under revision*: Tubaldi, F., Turella, L. , Pierno, A., Grodd, W, Tirindelli, R., & Castiello, U. Smelling odours, understanding actions. *Social Neuroscience.*

7. 1 INTRODUCTION

Neurophysiological research on neural processing underlying the understanding of others' actions has revealed activity within a network of brain regions including the premotor cortex, the primary motor and somatosensory cortices, several parietal areas, and the posterior temporal-occipital cortex (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Puce & Perret, 2003; Raos, Evangeliou, & Savaki, 2004; Raos, Evangeliou, & Savaki, 2007; Evangeliou, Raos, Galletti, & Savaki, 2009; Peeters et al., 2009). This motor circuitry, termed as the action observation system (AOS), enables the representation of the visual features characterizing the observed action (Rizzolatti, Fogassi, & Gallese, 2001; Keysers & Perret, 2004). For instance, when a monkey observes a human model grasping an object, the AOS exhibits a differential level of activity depending on the nature of both the visual object (e.g., edible vs. non edible; Fogassi et al., 2005) and the acting model (e.g., an entire model vs. an arm/hand ensemble; Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005). Furthermore, activity within this system appears to be modulated by the interaction between the target object and the moving effector. Responses in the monkey AOS differ depending on whether the monkey observes a human hand performing a proper grasp or observes a mimed grasp (Umiltà et al., 2001; Nelissen et al., 2005).

A recent advance in the characterization of the AOS is the demonstration that most of this system is multimodal. It not only responds to action-related information conveyed via vision, but also via audition (Kohler et al., 2002; Keysers et al., 2003). When a monkey hears the sound generated by a hand contacting an object (e.g., hands breaking a peanut), the AOS is activated as if the hand-object interaction was 'seen' (Kohler et al., 2002). Importantly, the level of activation within the AOS varies depending on the type of heard actions (Kohler et al., 2002; Keysers et al., 2003). Hearing the sound of a hand grasping a ring elicited less AOS activity than hearing the sound generated by the two hands breaking a peanut (Kohler et al., 2002).

Recent neuroimaging evidence suggests that an AOS, similar to that of the monkey in many respects, may also exist in humans (Grafton et al., 1996; Decety et al., 1997; Hari et al., 1998; Buccino et al., 2001; Perani et al., 2001; Avikainen et al., 2002; Grèzes et al., 2003; Buccino et al., 2004; Grosbras & Paus, 2006; Gazzola et al., 2006; Gazzola et al., 2007; Gazzola & Keysers, 2009; Turella et al., 2009; Peeters et al., 2009). The human AOS can discriminate the features of an agent performing the observed action (e.g., robotic vs. biological agents) (Tai et al., 2004), the features of the object grasped by another person (e.g., cookie vs. disk) (Hamilton & Grafton, 2006) and the visual elements characterizing a motor sequence which brings to a specific goal (Hamilton & Grafton, 2008; Majdandžić et al., 2009). Furthermore, the analogy between human and monkey AOS is strengthened by the revelation that the human AOS is also multimodal in nature. Some evidence now suggests that the human AOS is engaged when a person hears, for example, the sound of somebody's hands ripping a paper sheet (Aziz-Zadeh et al., 2004; Gazzola et al., 2006; Etzel et al., 2008). And, when both visual and auditory information related to another individual's action is available, the recognition of the perceived action is enhanced (Keysers et al., 2003).

The demonstration of multimodal aspects characterizing the AOS makes it possible that information coming from sensory modalities other than vision and audition is processed and integrated within the AOS. In this respect, a preliminary investigation has focused on the contribution that the sense of smell might have on action understanding (Rossi et al., 2008). Here participants looked at the experimenter while performing a grasping action towards one of four different foods. In some circumstances, the odour associated with the edible target was presented and transcranial magnetic stimulation (TMS) was delivered on the 'hand' sector of the primary motor cortex (M1). The main result was that the amplitude of motor evoked potentials (MEPs) increased when the odour pertaining to the target of the observed action was administered (Rossi et al., 2008). This finding indicates that the olfactory component of others' actions enhances excitability of M1. On this basis, one might be tempted to infer that olfactory information enters the observer's AOS enabling action understanding. However, before this conclusion can be fully accepted, some important issues might be considered. First, TMS does not allow localization of the brain structures underlying MEPs facilitation. Specifically, MEPs facilitation reflects changes in neural activity which may originate within M1 as well as within any of the brain areas establishing excitatory connections with M1 (Fadiga, Craighero, & Olivier, 2005). Such excitatory connections may come from either AOS areas or brain regions which lie outside the AOS.

Therefore, evidence for the representation of an action embedding olfactory information (i.e., olfactorymotor information) within the AOS is still debatable. Second, even assuming that via TMS it would be possible to demonstrate that the AOS represents olfactorymotor information, this would not be sufficient to document that olfactory cues play an effective role in action understanding. In addition, specific evidence that the AOS can differentiate across similar actions on the basis of olfactory information should be provided.

In the present fMRI study we manipulated olfactory information during a task involving the observation of different actions. The experimental conditions are illustrated in Figure 7.1.1. For the *Grasping Visual* (GV) and for the *Static Visual* (SV) conditions, participants observed a hand grasping a visual object or resting alongside a visual object, respectively (see Figure 7.1.1a-d). By testing which voxels show greater activation for the GV than for the SV condition we defined the AOS concerned with visuomotor information. We examined this region for representation of olfactorymotor information. For the *Grasping Olfactory* (GO) and the *Static Olfactory* (SO) conditions, participants observed video-clips which were identical to those utilized for the GV and the SV conditions, but the object was signalled via olfaction (see Figure 7.1.1e-h). We reasoned that if the AOS is able to represent olfactorymotor information, then an increase in activation for the GO condition with respect to the SO condition should be found. In order to reveal whether visuomotor and olfactorymotor information might be integrated within the AOS, we implemented the *Grasping Visual-*

olfactory (GVO) and the *Static Visual-olfactory* (SVO) conditions. These were identical to the GV and the SV conditions except that during the observation of the video-clip an odour associated with the visual object was also delivered (see Figure 7.1.1i-l). If visuomotor and olfactorymotor information do integrate, then a subadditive model should account for the pattern of activation across the GVO, the GV, and the GO conditions (Beauchamp, 2005a; Laurienti, Perrault, Stanford, Wallace, & Stein, 2005). The experimental design also included a Grasping (G) condition, in which participants observed a mimed hand grasp movement, and a Static (S) condition, in which a static hand was presented (see Figure 7.1.1m-p). Critically, by comparing the activation increment for the G with respect to the S condition with the activation increment for the GO with respect to the SO condition, we assess whether the AOS differentiated between a mimed hand grasp movement and a hand grasping an 'olfactory' target-object. If action discrimination occurs, then this process can solely be ascribed to the olfactory information which signalled the target-object. This is because both the amount and the type of perceived movement (e.g., hand shaping and trajectory, digits' opening and closing) are identical for the compared actions. In turn, the role played by olfactory information in action understanding would be demonstrated.

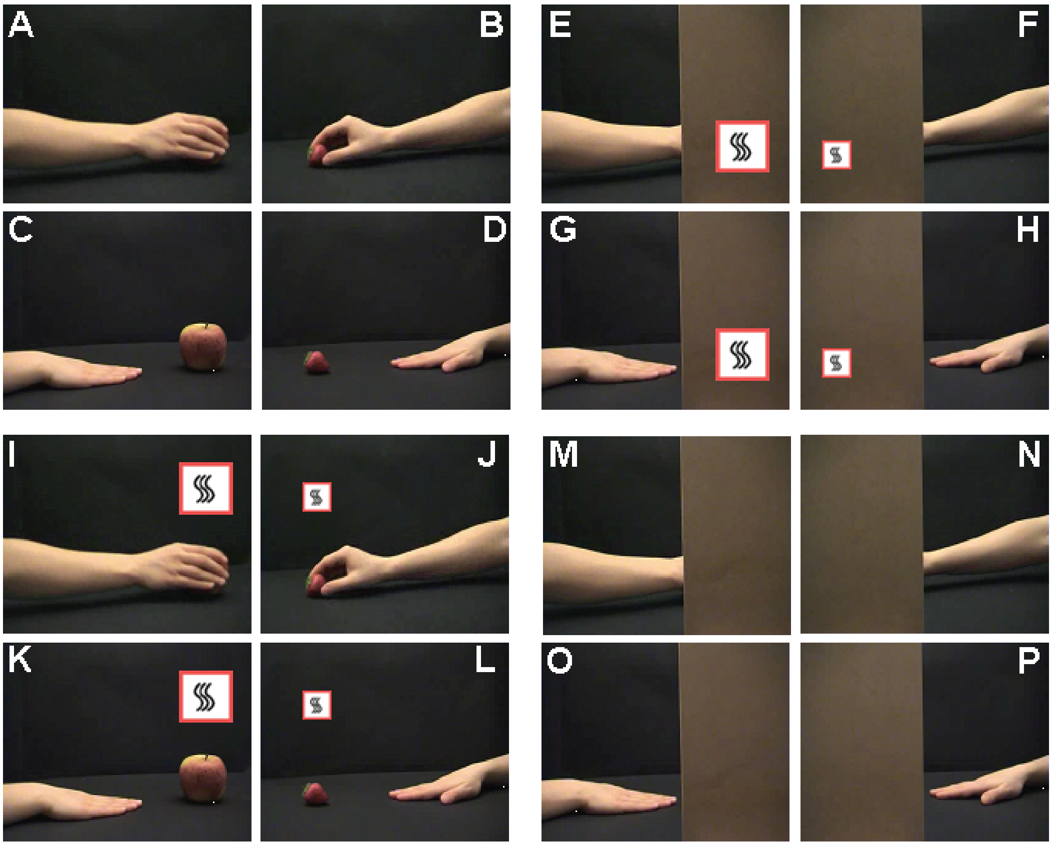

Figure 7.1.1 Graphical representation of the experimental conditions. *Grasping Visual* condition: (A) A whole hand grasp (WHG) for the large visual object and (B) a precision grip (PG) for the small visual object. *Static Visual* condition: A hand resting nearby (C) a large visual object and (D) a small visual object. *Grasping Olfactory* condition: A hand grasping either (E) a large object or (F) a small object hidden behind a partition in the presence of an odour associated with the object. *Static Olfactory* condition: A hand resting alongside either (G) a large object and (H) a small object hidden behind a partition in the presence of the odour associated with the object. *Grasping Visual-olfactory* condition: A hand grasping either (I) a large visual object and (J) a small visual object in the presence of the odour associated with the object. *Static Visual-olfactory* condition: a hand resting alongside (K) a large visual object and (L) a small visual object in the presence of the odour associated with that object. *Grasping* condition: A hand grasping either (M) a large object or (N) a small object hidden behind the partition. *Static* condition: A hand resting alongside either (O) a large object and (P) a small object hidden behind the partition. The boxes with red perimeters indicate the presence of an odour. The size of the boxes represents the size of the object evoked by the odour. The larger boxes indicate large objects. The smaller boxes indicate small objects.

7.2 METHODS

7.2.1 Participants

Fifteen right-handed participants (8 females; mean age = 26, range age 22-33 years) took part in the experiment. The experimental session lasted approximately 90 min.

7.2.2 Activation paradigm

The activation paradigm adopted in the present experiment have been described within the 'General methods' section (see Chapter 2). There were eight experimental conditions:

1. A *Grasping Visual* (GV) condition, in which participants observed the hand grasping either a large or a small object in the absence of odour (see Figure 7.1.1a-b).

2. A *Static Visual* (SV) condition, in which participants observed the hand resting alongside one of the four visual objects presented in Figure 1A, in a prone position, with the palm towards the working surface in the absence of odour (see Figure 7.1.1c-d).

3. A *Grasping Olfactory* (GO) condition in which participants observed a hand grasping an object as for the GV condition, but the object was hidden behind a brown coloured partition. During the observation of the video-clip an odour associated

with the hidden object was delivered (see Figure 7.1.1e-f; the boxes within Panels e-f indicate the presence of odour).

4. A *Static Olfactory* (SO) condition, in which participants observed a stationary hand as for the SV condition, but the object was hidden behind a brown coloured partition. During the observation of the video-clip an odour associated with the hidden object was delivered (see Figure 7.1.1g-h; the boxes within Panels g-h indicate the presence of odour).

5. A *Grasping Visual-olfactory* (GVO) condition, in which participants observed video-clips identical to those utilized for the GV condition except that during the observation of the video-clip an odour associated with the visual object was also delivered (see Figure 7.1.1 i-j; the boxes within Panels i-j indicate the presence of odour).

6. A *Static Visual-olfactory* (SVO) condition, in which participants observed video-clips identical to those utilized for the SV condition except that during the observation of the video-clip an odour associated with the visual object was also delivered (see Figure 7.1.1k-l; the boxes within Panels k-l indicate the presence of odour).

7. A *Grasping* (G) condition, in which participants observed video-clips identical to those utilized for the GO condition

except that during the observation of the video-clip no odour was delivered (see Figure 7.1.1m-n). Therefore, participants were presented with mimed hand grasp movements, i.e., hand grasping movements without a real end-goal.

8. A *Static* (S) condition, in which participants observed video-clips identical to those utilized for the SO condition except that during the observation of the video-clip no odour was delivered (see Figure 7.1.1o-p).

Participants' point of view within the scanner was also considered. Therefore, in half of the video-clips the hand entered the scene from the left, whereas in the other half the hand entered the scene from the right side (see Figure 7.1.1a-p). This resulted in a total of eight different experimental stimuli (i.e., four different objects by two different hand positions) per condition. This set of experimental stimuli was repeated four times within each condition (i.e., 32 stimuli corresponding to 32 experimental trials were administered).

7.2.3 Stimuli and apparatus

Stimuli and apparatus used in the present experiment have been described within the 'General methods' section (see Chapter 2).

7.2.4 Data acquisition

Imaging parameters for data acquisition have been described within the 'General methods' section (see Chapter 2).

7.2.5 Data pre-processing

The spatial pre-processing procedure adopted in the present investigation has been detailed within the ‘General methods’ section (see Chapter 2).

7.2.6 Data analysis

Both single-subject analysis and estimation of the statistical model for the group-analysis have been described within the ‘General methods’ section (see Chapter 2).

7.2.6.1 Region of interest (ROI) analysis

The hypotheses underlying the present study were concerned with the possibility that the AOS represented olfactorymotor information (either in isolation or in combination with visuomotor information) and used the olfactory component of this information for action discrimination. Therefore, testing for these hypotheses was confined to the relevant neural system, i.e., the AOS. We localized the AOS concerned with visuomotor information by performing the contrast GV > SV at whole brain level [intensity threshold, $P = 1.5\times10^{-2}$ FDR-corrected; cluster-extent threshold = 15 voxels, see Chapter 2] (Friston, Rotshein, Geng, Sterzer, & Henson, 2006; Friston & Henson, 2006; Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). Then, the voxel showing maximum activity within each of the identified areas was considered as a ROI (Friston et al., 2006; Saxe, Brett, & Kanwisher, 2006; Kilner, Neal, Weiskopf, Friston, & Frith, 2009). Because functional data were smoothed, the peak-voxel can be regarded as a ROI which corresponds to the smoothing kernel centred on that voxel (Friston et al., 2006; Saxe et al., 2006). By using Marsbar SPM Toolbox (Brett, Anton, Valabregue, & Poline, 2002) for each participant, the beta value corresponding to each experimental condition was extracted from each ROI. We verified the experimental hypotheses by performing statistical comparisons on these beta values. First, to evaluate whether the AOS represented olfactorymotor information, we tested for an increase in activation for the GO condition compared with the SO condition [GO > SO, intensity threshold, $P = 5 \times 10^{-2}$]. Second, to ascertain whether or not visuomotor and olfactorymotor information integrated within the AOS, we first tested whether there was an increase in activation in the GVO condition compared with the SVO condition [GVO > SVO, intensity threshold, $P = 5 \times 10^{-2}$]. Next, we evaluated whether such an activation increment was less than the sum of the activation increments for the GV and the GO conditions (Beauchamp, 2005a; Laurienti et al., 2005). In estimating this subadditive model, the appropriate control condition (i.e., the SV and the SO conditions, respectively) was subtracted from each experimental condition. This resulted in the interaction contrast: GVO – SVO < [GV – SV] + [GO – SO]. At this stage, we adopted a conservative intensity threshold ($P = 2.5 \times 10^{-2}$) to limit the possibility of false positives when testing an interaction contrast (i.e., GVO – SVO < [GV – SV] + [GO – SO]) within ROIs identified by performing a no orthogonal contrast (i.e., GV > SV) (Friston et al., 2006). Third, we assessed whether two similar actions could be differentiated within the AOS on the basis of olfactory information. To this end, we first tested whether an increase in activation for the G condition compared with the S condition occurred [G > S, intensity threshold, $P = 5\times10^{-2}$] within the AOS areas which also exhibited the activation increment GO > SO. Following this, we tested whether the activation increment G > S was different to the activation increment GO > SO [GO − SO > G − S and its reverse: GO − SO < G − S, intensity threshold, $P = 5\times10^{-2}$]. A t-test was performed for each contrast.

7.3 RESULTS

7.3.1 Identification of the AOS concerned with visuomotor information

The comparison GV > SV showed that perception of a hand grasping a visual object (i.e., visuomotor information) increased the level of activation within a network of brain regions distributed across the temporal, the parietal and the frontal lobes (see Figure 7.3.1.1 and Appendix E). With respect to the temporal lobe, activation increments of 4.51 % (S.E. = 0.64 %) and of 4.60 % (S.E. = 0.64 %) were evident within both the right and the left middle temporal cortex (MTc), respectively (see Figure 7.3.1.2a-b and Appendix E). When considering the superior parietal cortex (SPc), activation increments of 1.43 % (S.E. = 0.29 %) and of 2.35 % (S.E. = 0.37 %) were found within both the right and the left primary somatosensory area, respectively (see Figure 7.3.1.2c-d and Appendix E). With respect to the inferior parietal cortex (IPc), activation increments of 1.62 % (S.E. = 0.38 %) and of 1.71 % (S.E. = 0.49) were evident within both the right and the left sector PFcm, respectively (see Figure 7.3.1.2e-f and Appendix E). Parietal activity within the left sector PFcm spread within the intraparietal sulcus (Appendix E). An increase in activation of 0.87 % (S.E. = 0.17 %) was also detected within the sector PFt of the left IPc (see Figure 7.3.1.2g and Appendix E). When considering the frontal lobe, activation increased by 1.29 % (S.E. = 0.39 %) and 1.22 % (S.E. = 0.29 %) within both the right and the left premotor dorsal cortex (PMdc), respectively (see Figure 7.3.1.2h-i and Appendix E). Finally, an increase in activation of 1.04 % (S.E. = 0.26 %) was found within the right premotor ventral cortex (PMvc) (see Figure 7.3.1.2j and Appendix E).

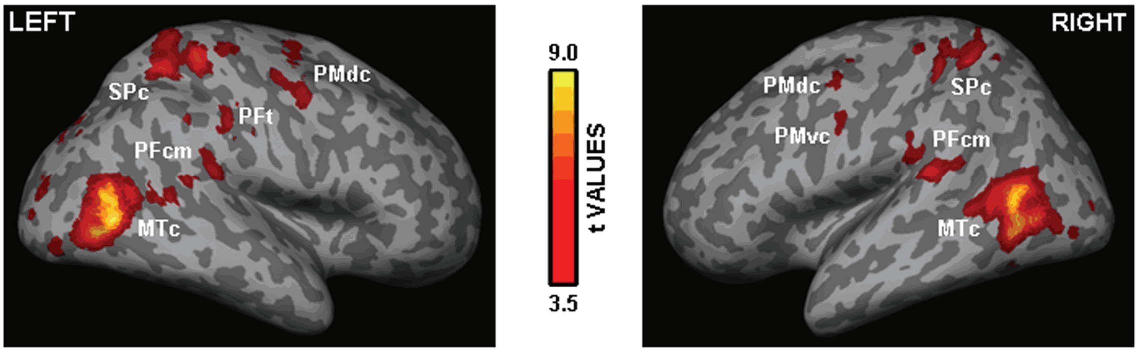

Figure 7.3.1.1 SPM {t} map resulting from the contrast GV > SV rendered onto the MNI canonical brain. Abbreviations for the activation clusters are as follows: MTc = middle temporal cortex, PFcm = ventral part of the anterior inferior parietal lobule; PFt = dorsal part of the anterior inferior parietal lobule; SPc = superior parietal cortex; PMdc = premotor dorsal cortex; PMvc = premotor ventral cortex.

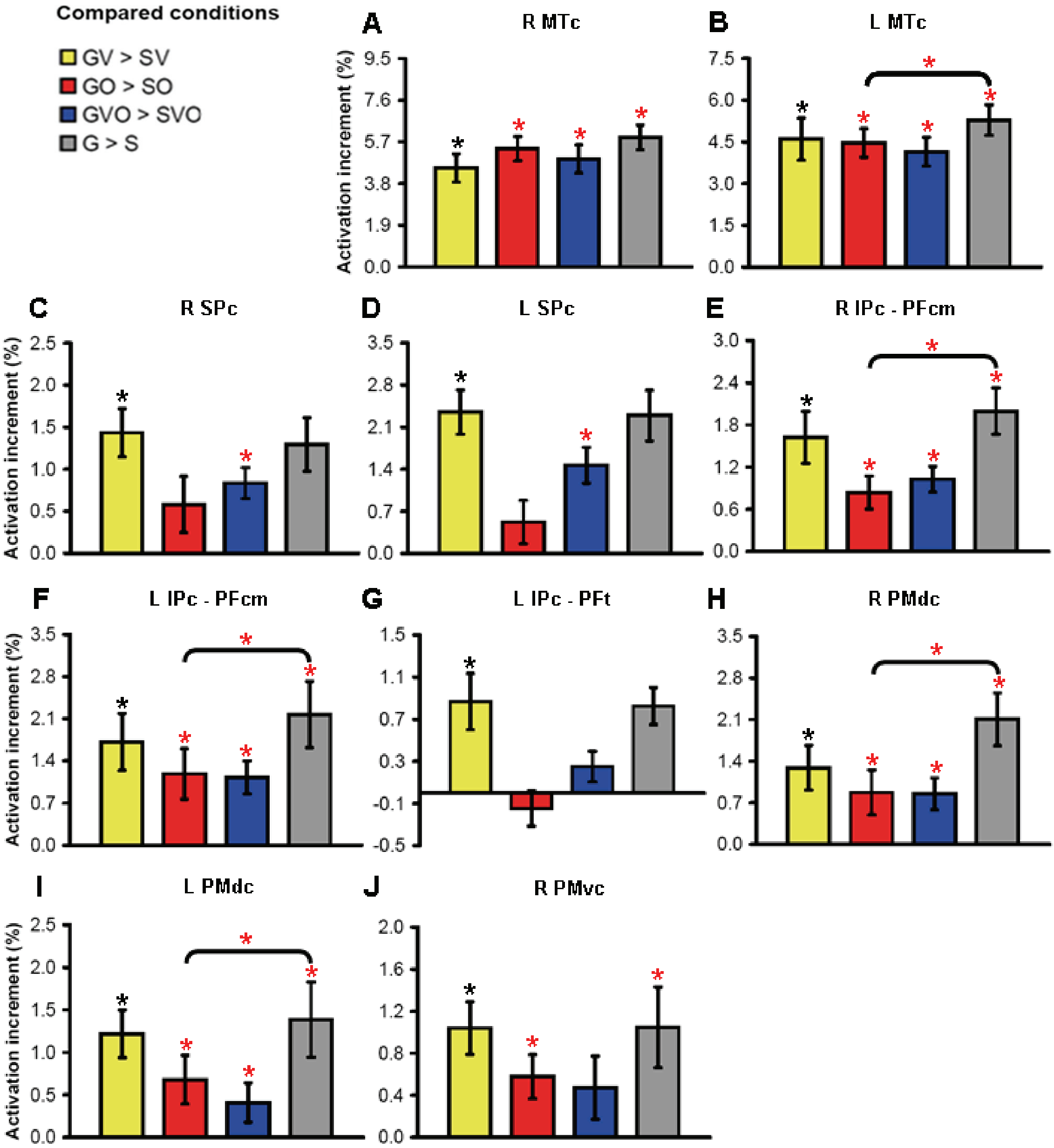

Figure 7.3.1.2 Functional modulation of the AOS activity depending on the nature of sensorymotor information. (A-J) Size of the increment in activation for the GV (yellow bars), the GO (red bars), the GVO (blue bars), and the G (grey bars) conditions with respect to the SV, the SO, the SVO, and the S conditions, respectively, as measured at the peak-voxel level within (A-B) the right and the left middle temporal cortex (R MTc and L MTc, respectively), (C-D) the right and the left superior parietal cortex (R SPc and L SPc, respectively), (E-F) the sector PFcm of the right and the left inferior parietal cortex (R IPc - PFcm and L IPc - PFcm, respectively), (G) the sector PFt of the left inferior parietal cortex (L IPc - PFt), (H-I) the right and the left premotor dorsal cortex (R PMdc and L PMdc, respectively), and (K) the right premotor ventral cortex (R PMvc). Error bars represent standard errors of the activation increments. Black asterisks indicate the statistically significant results obtained from the contrast GV › SV performed at whole brain level. Red asterisks indicate statistically significant results obtained from the ROI analysis for the contrasts GO › SO, GVO › SVO, G › S, and G – S › GO – SO.

7.3.2 Representation of olfactorymotor information within the AOS

The comparison GO > SO showed that perception of a hand grasping an olfactory object signalled via olfaction (i.e., olfactorymotor information) increased the level of activation within a subset of the cerebral areas identified for visuomotor information (see Figure 7.3.1.2a-j). Specifically, perceiving olfactorymotor information brought an increase of activation within both the right and the left MTc by 5.40 % (S.E. = 0.56 %; t = 9.32, $P = 1 \times 10^{-7}$) and 4.46 % (S.E. = 0.52 %; t = 8.36, $P = 4 \times 10^{-7}$), respectively (see Figure 7.3.1.2a-b). When considering the parietal lobe, activity did not increase within the bilateral SPc (right side: 0.58 %, S.E. = 0.33 %; t = 1.67, $p = 6 \times 10^{-2}$; left side: 0.52 %, S.E. = 0.36 %; t = 1.39, $P = 9 \times 10^{-2}$) (see Figure 7.3.1.2c-d). Whereas, activation increments of 0.84 % (S.E. = 0.24 %; t = 3.47, $P = 2 \times 10^{-3}$) and 1.18 % (S.E. = 0.43 %; t = 2.73, $P = 8 \times 10^{-3}$) were found within both the right and the left sector PFcm of the IPc, respectively (see Figure 7.3.1.2e-f). Finally, activation increment was not evident within the sector PFt of the left IPc (-0.15 %, S.E. = 0.17 %; t = -0.84, $P = 9 \times 10^{-1}$) (see Figure 7.3.1.2g). With respect to the frontal lobe, activity increased by 0.87 % (S.E. = 0.39%; t = 2.25, $P = 2 \times 10^{-2}$) and 0.68 % (S.E. = 0.30 %; t = 2.31, $P = 2 \times 10^{-2}$) within both the right and the left PMdc, respectively (see Figure 7.3.1.2h-i). An activation increment of 0.58 % (S.E. = 0.22 %; t = 2.69, $P = 9 \times 10^{-3}$) was also evident within the right PMvc (see Figure 7.3.1.2j).

7.3.3 Integration of visuomotor and olfactorymotor information within the AOS

The comparison GVO > SVO showed that perceiving a hand grasping an object signalled via both vision and olfaction, i.e., visuo-olfactorymotor information, determined activation increments within the bilateral MTc (right side: 4.92 %, S.E. = 0.64 %; t = 7.44, $P = 2\times10^{-6}$; left side: 4.15 %, S.E. = 0.72 %; t = 7.75, $P = 1\times10^{-6}$) (see Figure 7.3.1.2a-b), the bilateral SPc (right side: 0.83 %, S.E. = 0.18 %; t = 4.39, $P = 3\times10^{-4}$; left side: 1.47 %, S.E. = 0.30 %; t = 4.77, $P = 2\times10^{-4}$) (see Figure 7.3.1.2c-d), and the sector PFcm of the bilateral IPc (right side: 1.03 %, S.E. = 0.19 %; t = 5.47, $P = 4\times10^{-5}$; left side: 1.12 %, S.E. = 0.28 %; t = 3.69, $P = 1\times10^{-3}$) (see Figure 7.3.1.2e-f). With respect to the sector PFt of the left IPc, no activation increment was found (0.25 % S.E. = 0.14 %; t = 1.69, $P = 6\times10^{-2}$) (see Figure 7.3.1.2g). An activation increment was also evident for the bilateral PMdc (right side: 0.85 %, S.E. = 0.28 %; t = 3.07, $P = 4\times10^{-3}$; left side: 0.41 %, S.E. = 0.24 %; t = 1.73, $P = 5\times10^{-2}$) (see Figure 7.3.1.2h-i). Whereas, activity did not increase within the right PMvc (0.47 %, S.E. = 0.30 %; t = 1.52, $P = 8\times10^{-2}$) (see Figure 7.3.1.2j). The subadditive model [GVO − SVO] < [GV − SV] + [GO − SO] accounted for activation increments elicited by perception of visuo-olfactorymotor information. Specifically, activation increment within the right MTc for visuo-olfactorymotor information was 4.98 % less than the sum of activation increments for visuomotor and olfactorymotor information (-4.98 %, S.E. = 0.48 %) (Appendix F). A similar pattern of activation was also found for the left MTc (-4.91 %, S.E. = 0.30 %), the bilateral SPc (right side: -1.18 %, S.E. = 0.27 %; left side: -1.40 %, S.E. = 0.31 %), the sector PFcm of the bilateral IPc (right side: -1.44%, S.E. = 0.42%; left side: -1.77%, S.E. = 0.58%), and the bilateral PMdc (right side: -1.31%, S.E. = 0.57%; left side: -1.49%, S.E. = 0.45%) (Appendix F).

7.3.4 Representation of olfactory information within the AOS

The comparison G > S showed that the perception of a mimed grasp increased activation within the areas of the AOS which were also activated for olfactorymotor information (see Figure 7.3.1.2a-j). Specifically, activation increments within the bilateral MTc (right side: 5.91 %, S.E. = 0.57 %; t = 10.08, $P = 4\times10^{-8}$; left side: 5.29 %, S.E. = 0.55 %; t = 9.32, $P = 1\times10^{-5}$) (see Figure 7.3.1.2a-b), the sector PFcm of the bilateral IPc (right side: 2 %, S.E. = 0.34 %; t = 5.84, $P = 2\times10^{-5}$; left side: 2.17 %, S.E. = 0.57 %; t = 3.82, $P = 1\times10^{-3}$) (see Figure 7.3.1.2e-f), and the bilateral PMdc (right side: 2.10 %, S.E. = 0.46 %; t = 4.59, $P = 2\times10^{-4}$; left side: 1.39 %, S.E. = 0.46 %; t = 3.03, $P = 5\times10^{-3}$) (see Figure 7.3.1.2h-i) were evident. Activity also increased within the right PMvc by 1.05 % (S.E. = 0.40 %; t = 2.64, $P = 1\times10^{-2}$) (see Figure 7.3.1.2j). Crucially, the interaction contrast [GO – SO] < [G – S] indicated that perceiving olfactorymotor information brings an increase in activation which was different to that obtained while perceiving a mimed grasp. Specifically, activation increment within the left MTc for olfactorymotor information was 0.82 % less than that obtained for a mimed grasp (S.E. = 1.62 %; t = 1.96, $P = 4\times10^{-2}$) (see Figure 7.3.1.2b). A similar pattern of activation was also evident for the sector PFcm of the bilateral IPc (right side: -1.16 %, S.E. = 0.37 %; t = 3.09, $P = 4\times10^{-3}$;

left side: -0.99 %, S.E. = 0.42 %; t = 2.35, $P = 2 \times 10^{-2}$) (see Figure 7.3.1.2e-f), and the bilateral PMdc (right side: -1.23 %, S.E. = 0.36 %; t = 3.40, $P = 2 \times 10^{-3}$; left side: -0.71 %, S.E. = 0.39 %; t = 1.83, $P = 4 \times 10^{-2}$) (see Figure 7.3.1.2h-i). No differential activation was found for the right MTc (-0.51 %, S.E. = 1.20 %; t = 1.65, $P = 6 \times 10^{-2}$) (see Figure 7.3.1.2a) and the right PMvc (-0.47 %, S.E. = 0.31 %; t = 1.12, $P = 1 \times 10^{-1}$) (see Figure 7.3.1j).

7.4 DISCUSSION

The present experiment investigated the impact of olfactory information embedded in others' actions upon the AOS, a network of brain areas thought to be responsible for action understanding (Goldman & Sebanz, 2005; Raos et al., 2007). The obtained results demonstrate that olfactory cues are pivotal in determining neurofunctional modulation within such system.

7.4.1 The contribution of olfaction to action understanding

We show that the perception of a motor interaction involving a hand in contact with an 'olfactory' object has the potential to increase activity within the bilateral middle temporal cortex (MT/V5 complex), the bilateral inferior parietal cortex (sector PFcm), the dorsal part of the bilateral premotor cortex, and the ventral part of the right premotor ventral cortex. This provides compelling evidence that the AOS is able to build up representations of others' action embedding sensory cues conveyed via olfaction (Rossi et al., 2008).

Furthermore, we reveal that for a subset of these brain areas the level of activity for a hand grasping an 'olfactory' object was less than for a mimed grasp. Therefore, the AOS can also differentiate between actions on the basis of olfactory information.

A similar pattern of activation for the premotor and the inferior parietal cortices (sector PFcm) together with the intraparietal sulcus has been previously documented for the observation of a hand grasping a visual object with respect to the observation of a hand mimicking a grasp movement (Grèzes et al., 2003). Our findings confirm and extend the notion that a proper grasp and an identical non-object related movement are represented within the same network of temporal, parietal, and frontal areas. Noticeably, direct knowledge of what another individual is doing would reflect on the functional responses of this network (Thioux, Gazzola, & Keysers, 2008). Therefore, similarly to vision, the sense of smell might convey useful sensory information for understanding whether the perceived action is transitive (i.e., grasping an object) or intransitive (i.e., pretending to grasp an object). The fact that the AOS was more engaged for a mimed than for a proper grasp might suggest that although a similar network mediates the representation for both types of action, the neural responses differentiate these two types of action. Representation of a mimed grasp could be more complex and demanding than representation of a proper grasp. Representing a mimed grasp might imply the retrieval of the representation for a type of proper grasp which more closely match the mimed grasp (Villarreal et al., 2008). This process, in turn, might require the implementation of an image of the object which is based on movement cues (e.g., hand shaping) as if the perceived action was transitive (Villarreal et al., 2008). Conversely, the representation of a proper grasp would not be mediated by retrieval of a transitive action - to which the perceived action is to be matched, nor by 'object imagery'. Therefore, higher activity for a mimed than for a proper grasp would reflect the unusual nature of the perceived action and the richness of the observer's own sensorimotor experience.

A point worth mentioning is that action discrimination did not occur within the right ventral premotor cortex. This area responded similarly to both olfactorymotor information and a mimed grasp. It is possible that at this level there is a distinct type of analysis of others' action. That is, the ventral premotor cortex might be sensitive to how an individual performs an action, disregarding the goal and the intended effects of the action (Thioux et al., 2008). At this level, olfactory information, which signals the presence/absence of the target-object, would not be coded. Continuing on this analysis, because actions to grasp an 'olfactory' object and to mime a grasp movement were performed in a similar fashion, the representation of a proper grasp and a mimed grasp would not elicit discernable activity. A number of recent fMRI studies support this proposal (Buccino et al., 2001; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004; Sakreida, Schubotz, Wolfensteller, & von Cramon, 2005; Lui et al., 2008). Specifically, perception of both goal-directed action and mimes of the same actions without a visual object increased activity within the bilateral premotor cortex, with activity occurring within different sectors of the premotor cortex depending on the moving effector (hand, mouth, and foot; Buccino et al., 2001).

A further issue which needs to be discussed is concerned with how olfaction compares in terms of functions with other senses in humans. It is well known that olfaction provides us with detailed information about the world beyond our body surface (Stockhorst & Pietrowsky, 2004) and to recognize individuals, objects and events within the environment (Stevenson & Wilson, 2007). This perceptual function is the one most commonly associated with olfaction and a function which allows for a strict parallelism with other sensory modalities (Savic, Gulyas, Larsson, & Roland, 2000). In motor terms, recent evidence suggests that the effects of olfaction, similar to other modalities holds true for the execution of an action (Castiello et al., 2006; Tubaldi et al., 2008a,b; Tubaldi, Ansuini, Tirindelli, & Castiello, 2009). For instance, in the same way that viewing the fruit elicits action planning, smelling the odour of a fruit triggers the planning of a grasp suited for interacting with that fruit (Castiello et al., 2006; Tubaldi et al., 2008a). Further, when the type of grip evoked by the odour does not coincide with that for the to-be-grasped fruit, interference effects are evident on hand kinematics (Tubaldi et al., 2008a). Here we go a step further by revealing that these parallel qualities across the modalities are also evident at the level of action understanding. Olfaction, as in the visual and the auditory modalities, has the ability to code information regarding others' actions in a format which is fully manageable by the AOS.

7.4.2 Integration of visuomotor information with olfactorymotor information

Some studies in monkeys uncovered that the premotor cortex discharged when the animal either saw a hand acting upon a visual target-object (i.e., visuomotor information) or heard the sound related to such interaction (i.e., audiomotor information) (Kohler et al., 2002; Keysers et al., 2003). Importantly, the contributions of visuomotor and audiomotor information to the neuronal population activity were not independent, and when both pieces of sensorimotor information were available, the representation of another individual's action was optimal (Keysers et al., 2003). Subsequent investigations seemed to suggest that a similar integration mechanism might operate in humans (Gazzola et al., 2006; Etzel et al., 2008). Here we crucially extend the boundaries of the (multi)sensory motor territory within which this process occurs by demonstrating the contribution of the olfactory cues embedded into others' actions. The present findings show that the AOS responded when visuomotor and olfactorymotor information co-occurred (i.e., visuo-olfactorymotor information). This indicates that the two kinds of sensorimotor information are processed in concert, raising the possibility that an integration mechanism operates within the AOS. Evidence supporting this comes from our finding that the AOS exhibited a subadditive activation pattern when visuomotor and olfactorymotor information are presented simultaneously (i.e., the GVO condition) (Beauchamp, 2005a; Laurienti et al., 2005). The sum of the functional responses for each type of sensorimotor input (i.e., the GV and the GO conditions) did not predict the level of activity evoked by the condition in which both visuomotor and olfactorymotor information was present. Therefore, when visuomotor and olfactorymotor information were both available some form of interaction occurred, and the level of activity reflected a new visuo-olfactorymotor product, synthesized from visuomotor and olfactorymotor information. Along these lines, our results suggest that the fusion of visuomotor and olfactorymotor information may increase the likelihood of identifying others' actions or speed up action recognition (Oztop & Arbib, 2002; Bonaiuto, Rosta, & Arbib, 2007).

When considering AOS activity in greater detail, it emerges that the integrative areas fall within two distinct functional categories. The first category included the sector PFcm of the bilateral inferior parietal cortex, the bilateral premotor dorsal cortex, and the bilateral middle temporal cortex. These areas not only exhibited a subadditive pattern for visuo-olfactorymotor information, but also responded to both visuomotor and olfactorymotor information when presented in isolation. Therefore, any evidence of action, be it visuomotor or olfactorymotor, was sufficient per se to elicit a full-blown representation of the action. In this view, subadditive activity for visuo-olfactorymotor information would indicate the combination of two originally distinct representations, each based on specific types of sensorimotor information. The second functional category included the bilateral superior parietal cortex. This area was sensitive to visuomotor information, but it was not responsive to olfactorymotor information. Therefore it is unlikely that subadditive activity indicates the combination of visuomotor and olfactorymotor action representation. In this respect, we suggest that the superior parietal cortex represents other's people action based on visuomotor information and information conveyed via olfaction enriches such representation. Subadditive activity would reflect this process of sensorymotor enrichment.

Two further points regarding the present findings should be noted. First, they make a novel contribution to the mapping of convergence zones within the primate brain which might allow for the integration of signals from different senses. Previous cell recordings, tracing work, and neuroimaging studies (Stein & Stanford, 2008; Driver & Noesselt, 2008) strongly indicate that premotor and inferior parietal cortices receive converging feed-forward projections from visual, auditory, and somatosensory areas as to merge incoming information for object recognition and attentional orienting. In this connection, we show that the synergy among percepts also involves olfactorymotor and visuomotor information and, most importantly, such synergy contributes to a meaningful representation of ecologically relevant actions. Second, subadditive activity was found within the middle temporal cortex. Recent neuroimaging investigations have shown that motion cues conveyed via different sensory modalities are represented within the middle temporal cortex (Born & Bradley, 2005; Bartels, Logothetis, & Moutoussis, 2008; Hagen et al., 2002; Alink, Singer, & Muckli, 2008; Scheef et al., 2009). Furthermore, the middle temporal cortex is able to integrate visual, auditory and tactile motion cues in order to stabilize and enhance motion perception (Beauchamp, 2005b). Visuomotor and olfactorymotor information can be regarded as complex patterns which specify the motion of the reach-to-grasp toward the object. Therefore, the finding that these patterns do integrate confirms the role of the middle temporal cortex in multimodal motion integration, and extends it to the olfactory domain.

A final point is concerned with the locus within which visuomotor and olfactorymotor information integrate. Previous evidence indicates that when the task is to detect the odour of a visible object, then olfactory and visual information are integrated within multisensory centres sub-serving object recognition, namely the orbitofrontal cortex (Gottfried & Dolan, 2003; Österbauer et al., 2005). However, when the task is to localize the source of the odour, then olfactory information is encoded within the superior temporal gyrus, an area within which multimodal spatial maps are represented (Porter, Anand, Johnson, Khan, & Sobel, 2005). Here we add to this literature by demonstrating that when the task requires observation of a goal-directed action, visual-olfactory binding occurs within the various components of the AOS. Hence we provide further fuel to the notion that the main determinant for assigning the locus of sensorimotor integration is the nature of the task.

8. Conclusive remarks

Recent evidence has contributed to change the view according to which action representation chiefly depends on visual information. In particular, research on hand grasping actions has emphasized that a multimodal interplay across vision, audition, the sense of touch, and proprioception occurs when performing and understanding an action (e.g., Castiello, 1996; Patchay et al., 2003; Patchay et al., 2006; Gazzola et al., 2006; Zahariev & MacKenzie, 2007; Castiello et al., 2007; Etzel et al., 2008).

The experimental work included in the present thesis aimed at extending the multisensory aspects of action representation to the olfactory domain. I first addressed this issue from the perspective of action execution by asking participants to reach and grasp a target-object under different circumstances of visual and olfactory stimulation. The angular excursion at the level of individual digits, digits' angular distance, and arm movement duration were recorded. Next, I focused on action understanding by asking participants to observe others' grasping actions under different visual and olfactory conditions. Here, cerebral activity of the neural system responsible for action understanding, i.e., the Action Observation System (AOS) was recorded.

An overview of this experimentation, its implications for both the psychological and the neural mechanisms underlying multimodal representations of actions and some final considerations are outlined in the following sections.

8.1 The role of olfactory information in action performance and understanding

The results of the present thesis indicate that fingers are differently moulded depending on the ‘size’ of an olfactory-encoded object (Chapter 3). This finding is in line with previous evidence showing that there is a strong relationship between the posture assumed by the hand and the object structure conveyed via vision, audition, and the sense of touch (e.g., Castiello, 1996; Patchay et al., 2003; Patchay et al., 2006; Zahariev & MacKenzie, 2007; Castiello et al., 2007). However, I also found an indication that odour ‘size’ is not the sole olfactory aspect that the CNS takes into account when performing a hand grasping action. As shown in Chapters 4 and 5, odours also affected temporal parameterization of arm-movement depending on the relationship between the accuracy embedded within the ‘grasp’ motor plan elicited by an odour and the functional demands required for a successful action. In this respect, it can be concluded that olfactory information leaks in the motor control system and enables planning and execution of action in terms of both object geometry and action goal.

When considering the understanding of other’s actions, the fMRI findings reported in Chapter 7 of the present thesis indicate that the AOS uses olfactory information to discriminate between somebody’s hands grasping an object and somebody’s hands mimicking a grasping action. This signifies that olfactory information allows achieving an internal description of actions which, in turn, would enable action understanding. This result is line with previous evidence showing the multimodal nature of the AOS (Aziz-Zadeh et al., 2004; Gazzola et al., 2006; Etzel et al., 2008).

8.2 Possible neural mechanisms responsible for the effects of odour on action representation

Neurophysiological investigations in monkeys have established that the cortical motor system is not only endowed with cells discharging when the monkey performs actions (i.e., purely motor neurons) (Rizzolatti & Luppino, 2001). Specifically, neural sites located within the premotor cortex (PMc) include two classes of neurones with sensory properties. The purely sensory neurons, i.e., cells firing only when the monkey perceives some kind of stimulation, and the sensory-motor neurons, i.e., cells responding during both action performance and perceptual stimulation (Fogassi & Gallese, 2004). To date, purely sensory and sensory-motor neurons constitute the neural model used for explaining the effects that visual, auditory, and somatosensory information have on action planning and understanding in humans (e.g., Castiello, 1996; Patchay et al., 2003; Patchay et al., 2006; Gazzola et al., 2006; Zahariev & MacKenzie, 2007; Castiello et al., 2007; Etzel et al., 2008).

In first instance, bimodal sensory neurons which respond to both superficial tactile stimulation coming from different body parts and visual three-dimensional objects have been localized within the dorsal part of the PMc (Graziano, Yap, & Gross, 1994; Graziano, Hu, & Gross, 1997; Fogassi et al., 1996). These cells bind together somatosensory and visual attributes of a stimulus (Fogassi & Gallese, 2004). A subcategory of the bimodal sensory neurons can also be activated by acoustic stimuli introduced in the space around the monkey's head (i.e., trimodal neurons, Graziano, Reiss, & Gross, 1999). These polymodal cells would play a major role in the multimodal representation of objects within the motor system.

Furthermore, part of the bimodal neurons not only responds to objects approaching monkey's effectors but it also fires when the monkey moves such effectors (Gentilucci et al., 1988; Graziano et al., 1997). These neurons would allow retrieving a pragmatic representation of the action associated with the object entering into the work space of the monkey's effectors. Such a representation, if the context is suitable, can be turned into overt action upon that object, whereas, if not, it remains as potential action. Another pool of sensory-motor neurons which might turn objects into potential actions has been found within the ventral sector of the PMc (e.g., Gallese et al., 1996; Rizzolatti et al., 1996). These cells, labelled as canonical neurons, discharge when the monkey both perceive an object and act upon that object.

Finally, neurons which would map actions performed by another individual onto the observer's motor repertoire has been identified within the ventral PMc (e.g., Di Pellegrino et al., 1992; Rizzolatti et al., 1996). These sensory-motor cells, labelled as mirror neurons, discharge when the monkeys both see others' actions and perform similar actions. Recently, it has been demonstrated that mirror neurons can also be activated by auditory stimuli (Kohler et al., 2002; Keysers et al., 2003). They do not only respond to visual perception of actions but they are also sensitive to the sounds generated by other individual's actions (Kohler et al., 2002; Keysers et al., 2003).

Altogether these evidences indicate that the premotor cortex transforms sensory inputs conveyed via different modalities in order to accomplish both motor tasks (i.e., action planning and execution) and cognitive tasks (i.e., object representation and other's action representation). In this view, I suggest that the effects olfactory stimuli have on both action performance and understanding might be explained assuming that odours are processed by the PMc sensory and sensory-motor neurons. Further neurophysiological investigation in monkeys, neuroimaging and behavioural experiments in humans are necessary to validate this proposal.

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APPENDIX A

Average angular excursions at different epochs of normalized movement time. Mean standard errors are reported in parentheses. The relevant statistical comparisons are between the OL and the LL conditions and between the OL and the SL conditions.

	NORMALIZED MOVEMENT TIME (%)			
	10		20	
	OL	LL	OL	LL
JOINT				
Tmcp			-7 (2)	-8* (2.5)
Ipip	103 (2.5)	101.5* (2.5)	92.5 (2.5)	90.5** (3)
Mpip			66 (1.5)	64.5** (1.5)
Rpip	68 (1.5)	67* (1.5)	65 (1.5)	64** (2)

	NORMALIZED MOVEMENT TIME (%)							
	40		50		60		100	
	OL	SL	OL	SL	OL	SL	OL	SL
JOINT								
Imcp	-4 (4)	-2.5* (3)	-13 (3.5)	-11.5* (3.5)	-17 (3.5)	-16* (3.5)	-2 (3.5)	-1* (3.5)
Mmcp	2 (2)	3.5* (2)	-3.5 (2)	-2** (2)	-6 (2)	-5* (2)		
Rmcp			-9.5 (2)	-8.5** (2)				
Tpip			0 (1)	1** (1)				
Ipip	65 (3)	66.5* (3)						

Notes. Only significant results are reported (* = $P < 0.05$; ** = $P < 0.01$). OL = Odourless air-Large target; LL = Large odour-Large target; SL = Small odour-Large target. Tmcp = metacarpal joint of the thumb; Imcp = metacarpal joint of the index finger; Mmcp = metacarpal joint of the middle finger; Rmcp = metacarpal joint of the ring finger; Tpip = proximal interphalangeal joint of the thumb, Ipip = proximal interphalangeal joint of the index finger; Rpip = proximal interphalangeal joint of the ring finger.

APPENDIX B

Average fingers' abduction angles at different epochs of the normalized movement time. Mean standard errors are reported in parentheses. The relevant statistical comparisons are between the OL and the SL conditions.

	NORMALIZED MOVEMENT TIME (%)											
	50		60		70		80		90		100	
	OL	SL	OL	SL	OL	SL	OL	SL	OL	SL	OL	SL
ABDUCTION ANGLE												
MIDDLE-RING	-31 (1.5)	-30 (1.5)	-31.5 (2)	-30.5 (1.5)	-31.5 (2)	-30.5 (1.5)			-29.5 (2.5)	-28.5 (2)	-29 (2.5)	-27.5 (2.5)
RING-LITTLE							-30 (2.5)	-29 (2.5)				

Notes. Only significant results are reported ($P < 0.05$). OL = Odourless air -Large target; SL = Small odour-Large target.

APPENDIX C

Average angular excursions at different epochs of normalized movement time. Mean standard errors are reported in parentheses. The relevant statistical comparisons are between the OS and the SS conditions and the OS and the LS conditions.

	NORMALIZED MOVEMENT TIME (%)							
	20		40		50		60	
	OS	SS	OS	SS	OS	SS	OS	SS
JOINT								
Imcp			14 (3.5)	16* (3.5)				
Lmcp	-5 (2)	-4** (2)	-6 (2)	-5** (2)	-9 (2.5)	-8*** (2.5)	-12.5 (3)	-11.5** (3)

	NORMALIZED MOVEMENT TIME (%)															
	10		20		40		50		60		80		90		100	
	OS	LS	OS	LS	OS	LS	OS	LS	OS	LS	OS	LS	OS	LS	OS	LS
JOINT																
Tmcp	-6.5 (2)	-5.5** (2)			-10.5 (2)	-9.5* (2)	-12 (2)	-11*** (2)	-13.5 (2)	-12.5*** (2)	-14 (2)	-13* (2)	-13.5 (2)	-12.5* (2)	-13 (2)	-12** (2)
Rmcp			-1.5 (2)	-2.5* (2)												

Notes. Only significant results are reported ($* = P < 0.05$; $** = P < 0.01$, $*** = P < 0.001$). OS = Odourless air-Small target; SS = Small odour-Small target; LS = Large odour-Large target. Tmcp = metacarpal joint of the thumb; Imcp = metacarpal joint of the index finger; Rmcp = metacarpal joint of the ring finger; Lmcp = metacarpal joint of the little finger.

APPENDIX D

Average absolute value of the slopes of the regression lines fitting angular values for each articulations' pair at different epochs of normalized movement time. Mean standard errors are reported in parentheses.

NORMALIZED MOVEMENT TIME (%)							
40		50		60		70	
OL	SL	OL	SL	OL	SL	OL	SL
0.33 (0.02)	0.30 (0.02)	0.33 (0.02)	0.29 (0.02)	0.31 (0.02)	0.28 (0.02)	0.30 (0.02)	0.28 (0.02)

NORMALIZED MOVEMENT TIME (%)			
20		40	
OS	LS	OS	LS
0.34 (0.03)	0.33 (0.03)	0.34 (0.03)	0.30 (0.03)

Notes. Only significant results are reported ($P < 0.01$, *FDR*-corrected). OL = Odourless air-Large target; SL = Small odour-Large target; OS = Odourless air-Small target; LS = Large odour-Large target.

APPENDIX E

Anatomical localization of the activation peaks as revealed by the contrast *Grasping Visual* (GV) condition > *Static Visual* (SV) condition.

Contrast: GV > SV

Brain regions	x	y	z[a]	Probabilistic cytoarchitecture	Peak t	*P* value[b]
TEMPORAL LOBE						
Right middle temporal cortex	48	-66	4	MT/V5 (50%)	8.52	1×10^{-8}
Left middle temporal cortex	-46	-70	8	MT/V5 (30%)	9.06	1×10^{-8}
PARIETAL LOBE						
Right superior parietal cortex Primary somatosensory area	32	-48	58	BA 2 (60%)	5.47	6×10^{-5}
Left superior parietal cortex Primary somatosensory area	-34	-44	60	BA 2 (50%)	6.51	2×10^{-6}
Right inferior parietal cortex	56	-36	22	PF_{cm} (60%)	5.87	2×10^{-5}
Left inferior parietal cortex	-48	-38	26	PF_{cm} (50%) hIP2 (10%)	4.94	3×10^{-4}
Left inferior parietal cortex	-48	-24	36	PF_t (60%)	4.53	9×10^{-4}
FRONTAL LOBE						
Right dorsal premotor cortex	42	-4	54	BA 6 (40%)	3.92	5×10^{-3}
Left dorsal premotor cortex	-48	-4	48	BA 6 (100%)	4.56	9×10^{-4}
Right ventral premotor cortex	58	4	40	BA 6 (60%)	4.18	2×10^{-3}

[a] MNI coordinates (mm).

[b] FDR-corrected for whole-brain volume (probability threshold = 1.5×10^{-2} FDR-corrected).

Abbreviations for the cytoarchitectonic nomenclature are as follows: PF_{cm} = ventral part of the anterior inferior parietal lobule; PF_t = dorsal part of the anterior inferior parietal lobule; hIP2 = human intraparietal area 2 (Caspers et al., 2008)

APPENDIX F

Neural sites of integration between visuomtor and olfactorymotor information. Averaged activation across participants for the subadditive model is reported. Standard errors are shown in parentheses. Statistical assessment for the subadditive model is also presented.localization of the activation peaks as revealed by the contrast *Grasping Visual* (GV) condition › *Static Visual* (SV) condition.

Subadditive model: GVO – SVO ‹ (GV – SV) + (GO – SO)

	ROI analysis		
Brain regions	Averaged activation (%)[a]	t value	*P* value[b]
TEMPORAL LOBE			
Right middle temporal cortex MT/V5	-4.98 (0.48)	7.63	1×10^{-6}
Left middle temporal cortex MT/V5	-4.91 (0.30)	6.33	1×10^{-7}
PARIETAL LOBE			
Right superior parietal cortex BA 2	-1.18 (0.27)	4.39	3×10^{-4}
Left superior parietal cortex BA 2	-1.40 (0.31)	4.77	2×10^{-4}
Right inferior parietal cortex PF_{cm}	-1.44 (0.42)	3.43	2×10^{-3}
Left inferior parietal cortex PF_{cm}/hIP2	-1.77 (0.58)	3.05	4×10^{-3}
Frontal lobe			
Right dorsal premotor cortex BA 6	-1.31 (0.57)	2.31	2×10^{-2}
Left dorsal premotor cortex BA 6	-1.49 (0.45)	3.31	3×10^{-3}

[a] Subadditive combination of betas as measured at the peak voxel revealed by the contrast GV › SV.

[b] Corrected-probability threshold = 2.5×10^{-2}.

Abbreviations for the experimental conditions are as follows: GVO = Grasping Visual-olfactory condition; SVO = Static Visual-olfactory condition; GV = Grasping Visual condition; SV = Static Visual condition; GO = Grasping Olfactory condition; SO = Static Olfactory condition.