# Effects of Olfactory Stimuli on Arm-Reaching Duration

# Federico Tubaldi<sup>1</sup>, Caterina Ansuini<sup>1</sup>, M. Luisa Demattè<sup>2</sup>, Roberto Tirindelli<sup>3</sup> and Umberto Castiello<sup>1,4</sup>

<sup>1</sup>Department of General Psychology, University of Padua, Via Venezia 8, 35131, Padua, Italy, <sup>2</sup>Department of Cognitive Sciences and Education, Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068, Trento, Italy, <sup>3</sup>Department of Neuroscience, University of Parma, via Volturno, 39/E, 43100, Parma, Italy and <sup>4</sup>Department of Psychology, Royal Holloway, University of London, Egham, Surrey, TW027, London, UK

Correspondence to be sent to: Umberto Castiello, Department of General Psychology, University of Padua, Via Venezia 8, 35131, Padua, Italy. e-mail: umberto.castiello@unipd.it

# Abstract

The aim of the present study was to investigate the effects of olfactory stimuli on visually guided reaching. In Experiment 1, participants reached toward and grasped either a small (almond/strawberry) or a large (apple/orange) visual target. Any 1 of 4 odors corresponding to the visual stimuli or odorless air was administered before movement initiation. Within the same block of trials, participants smelled 1) an odor associated with an object of a different size than the target, 2) an odor associated with an object of a size equal to that of the target, or 3) odorless air. Results indicated that reaching duration was longer for trials in which the odor "size" and the visual target did not match than when they matched. In Experiment 2, the same procedures were applied but the "no-odor" trials were administered in a separate block to the "odor" trials. Similar results as for Experiment 1 were found. However, in contrast to Experiment 1, the presence of an odor 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 stimulus.

# Introduction

Several studies have now shown that selecting a target for a reach-to-grasp movement in the presence of task-irrelevant objects leads to interference effects on movement kinematics. For instance, Tipper et al. (1997) (see also Welsh and Elliott 2004) required subjects to initiate a reaching action as quickly as possible after a visual cue (either blue or green in color) had appeared followed by the presentation of 2 stimuli, a target (either a blue or green block) and a distractor (a red block), both similar in size but separately positioned at 1 of 4 different locations. Prior to the start of the experiment, the subjects had been instructed only to move (i.e., reach and grasp the target) if the target matched the cue's color. In such situations, distractors appear to compete for the control of action and interference emerged as revealed by an increase in reaching duration. In an attempt to specifically select the grasping component, Castiello (1999) asked participants to reach and grasp a target presented in conjunction with a task-irrelevant object of a different size, but positioned in roughly the same location and similar in color, to the target. It was found that the subjects' amplitude of peak grip aperture while en route to the target was influenced by the size of the task-irrelevant object. If the target was small, the amplitude of peak grip aperture was greater when the task-irrelevant object was large than when it was not present. Conversely, the amplitude of peak grip aperture for the grasp of a large target was less when the task-irrelevant object was small than when it was not present. Altogether, these studies suggest that multiple objects in a visual scene can evoke parallel motor processes, which trigger mutual interference.

The notion that multiple objects can evoke parallel activation of motor representations has also been tackled from a multisensory perspective, revealing that cross-modal links in motor control are substantial and numerous (Gentilucci et al. 1998; Patchay et al. 2003, 2006). In these studies, cross-modal links between haptic and visual information when reaching to grasp a visual target were investigated. Participants reached and grasped with one hand a visual target (sphere) presented in different sizes while grasping another unseen sphere of a different size in the other hand. The general result was that maximum grip aperture of a visually guided reach to grasp was proportional to the diameter of the distractor object manipulated proprioceptively with the other hand. Altogether, the reported effect seems to arise from cross-modal interference between 2 concurrent plans for object-oriented action.

The effects of multisensory coding during a natural grasping task have also been extended to the chemosensory modalities (Castiello et al. 2006). It was demonstrated that odor information can modulate a complex motor system such as that subtending hand grasping. When participants smelled an odor 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 odor 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). 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) 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 and Goodale 1991). Specifically, reaching duration increases for reach-to-grasp movements directed toward smaller compared with larger objects (Marteniuk et al. 1987; Gentilucci et al. 1991; Jakobson and Goodale 1991). Furthermore, remember that when reaching toward and grasping a smaller target in the presence of a larger task-irrelevant object 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" odor and increases for movements toward a large target in the presence of a "small" odor, then inference regarding the influence of odor "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 odor 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 et al. 1999; Zahariev and MacKenzie 2007). Therefore, it might well be that olfactory cues also determine a level of alertness which manifests in a shorter reaching duration. This inference finds some support from previous olfactory research suggesting that the presence of odors increases alertness in various tasks (Warm et al. 1991; Dember et al. 1995; Millot et al. 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 odors regardless of their pleasantness. Therefore, if the presence of olfactory information determines a generalized facilitatory effect, then such facilitation might also be evident in reaching duration.

#### **Experiment 1**

#### Materials and methods

#### Subjects

Twenty-six right-handed subjects (13 females and 13 males, mean age of 22 with standard error of the mean [SEM] of  $\pm 3.5$  years), who reported normal olfaction, no history of olfactory dysfunction, and normal or corrected-to-normal vision in a confidential report, gave their informed consent to participate in the present experiment. The experimental procedures were approved by the Institutional Review Board of the University of Padua and were in accordance with the Declaration of Helsinki. The experimental session lasted approximately 30 min.

#### Stimuli and apparatus

The target stimuli consisted of 2 large fruits, an apple and an orange, or 2 small fruits, an almond and a strawberry (Figure 1A). The administered odor stimuli corresponded to the target stimuli described above. Odor solutions of strawberry, almond, orange, and apple were obtained mixing 6000  $\mu$ l of prophylenic glycol and 180  $\mu$ l (3%), 60  $\mu$ l (1%), 420  $\mu$ l (7%), and 45  $\mu$ l (0.75%) of the specific odorant compound, respectively. A pilot study was conducted to ascertain that the objects associated with the odor stimuli were all correctly identified by the participants. Further, the odor stimuli were judged to have equal intensity, hedonic tone, and familiarity and to be isointense during all the experimental session. A custom-built computer-controlled olfactometer (Department of Experimental Psychology, University of Oxford) was used to deliver the odor stimuli or odorless air. Each



Figure 1 (A) The large (i.e., apple and orange) and the small (i.e., almond and strawberry) visual targets. (B) The experimental setup and the hand starting posture.

odor generator consisted of a glass boat containing 1 of the 4 odor stimuli. A fifth glass boat containing prophylenic glycol was used for the delivery of odorless air. The air passed over the odor solutions and the prophylenic glycol at a flow rate of 8 l/min and was delivered to subjects via Teflon tubing to a facial mask.

At the beginning of each trial, the subject's right hand was placed on a starting support within which was embedded a pressure switch, the starting switch. The hand starting support was designed with slight convexities dictating a natural flexed posture of the fingers (see the Initial hand position, Figure 1B). The target object was placed on a second pressure switch, the ending switch, embedded within the table surface (Figure 1B). Vision was controlled using spectacles fitted with liquid crystal lenses (Translucent Technologies Inc., Toronto, Ontario, Canada). Reaching forward released the starting switch, which resulted in making the target visible and defined the onset of the movement. Lifting the target object released the ending switch, which defined the offset of the movement. Reaching duration was measured as the time occurring from the release of the starting switch to the release of the ending switch.

#### Procedure

At the beginning of each experimental session, participants wore a facial mask (see Stimuli and apparatus section) and sat on a height-adjustable chair in front of a rectangular table with their right hand resting on the starting support. They were requested to reach toward, grasp, and lift a target object positioned at the center of the working surface at a distance of 33 cm from the starting switch (see Figure 1B). The event sequence for each trial was as follows: 1) vision was occluded before the target was positioned on the working surface; 2) an auditory tone (with 850-ms duration, 65-dB sound pressure, and 800-Hz frequency) indicated the odor delivery; 3) after 3 s, the tone indicated the offset of odor delivery; 4) following a 500-ms interval, the tone was presented again; 5) upon hearing the tone, participants were instructed to reach toward, grasp, and lift the target object. Sufficient time (10 s) was allowed between trials to recover from any odor adaptation (Hummel et al. 1996).

The reach-to-grasp task was performed under 6 different conditions. There were 2 conditions in which odorless air was delivered before initiating the action toward either the large or the small target. These conditions were termed "OL" and "OS", respectively. Further, before initiating the movement toward a large target, an odor associated with either a large or a small object could be delivered. These conditions were called "LL" and "SL", respectively. The conditions in which an odor associated with a small or a large object was delivered before starting the movement toward a small target were also considered ("SS" and "LS", respectively). 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.

#### Data analysis

We test our specific hypotheses by means of repeatedmeasures planned orthogonal contrasts following a 2 stages procedure (Furr and Rosenthal 2003). (When specific questions need to be investigated, planned orthogonal comparisons represent a better option than classical omnibus tests [e.g., analysis of variance] followed by post hoc unplanned comparisons [Keppel 1982]. Planned orthogonal comparisons not only provide greater statistical power against Type II error, because adjustments incorporated in post hoc procedures are not necessary, but also they allow for localizing the source of experimental effect. Furthermore, when using such approach, the total amount of variance is additively partitioned in the dependent variable [i.e., the outcome of each contrast does not depend on the outcome of a different contrast] allowing for straightforward and unambiguous interpretation of the results [Stevens 2002].) Because contrasts are coding vectors that mathematically express predicted results (Thompson 1985), we created vectors to assess whether reaching duration was 1) shorter when the to-begrasped object was large than when it was small (i.e., 1/3[OS + SS + LS] - 1/3[OL + LL + SL]), 2) shorter when an odor had been delivered than when no odor had been presented (i.e., 1/2[OS + OL] - 1/4[SS + LL + LS + SL]), 3) longer for a large target when the delivered odor was associated with a small object than when it was associated with a large object (i.e., 1 SL - 1 LL), and 4) shorter for a small target when the administered odor was associated with a large object than when it was associated with a small object (i.e., 1 SS - 1 LS). The t values corresponding to each contrast were considered statistically significant if less than 0.05 ( $\alpha$ -level).

#### **Results and discussion**

The analyses revealed that reaching duration was shorter when the object to be grasped was large than when it was small (large =  $1268 \pm 70$  ms; small =  $1348 \pm 65$  ms,  $t_{25} =$ -6.01, P < 0.001) (see Figure 2). Further, no significant differences were found when comparing reaching duration for trials in which no odor was delivered with reaching duration for trials in which an odor was presented (no odor =  $1314 \pm$ 70 ms; odor =  $1305 \pm 67$  ms,  $t_{25} = 0.67$ , not significant [NS]). Finally, as shown in Figure 2, reaching duration was longer for the SL (black bars) than for the LL (horizontal striped bars) condition (SL =  $1276 \pm 70$  ms; LL =  $1255 \pm 69$  ms,  $t_{25} =$ 1.70, P < 0.05). In contrast, reaching duration was not significantly different for LS (gray bars) and SS (vertically striped bars) conditions (LS =  $1352 \pm 64$  ms; SS =  $1334 \pm$ 67 ms,  $t_{25} = 1.16$ , NS) (see Figure 2).

These results partially confirm our hypothesis that there is an effect of the 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 odor than following the delivery of



**Figure 2** Mean reaching duration for OL (no odor–large target), SL (small odor–large target), LL (large odor–large target), OS (no odor–small target), LS (large odor–small target), and SS (small odor–small target) conditions in Experiment 1. Error bars indicate SEM. Asterisks indicate significant values (\*\*\* P < 0.001; \* P < 0.05).

a large odor. In contrast to our prediction, however, reaching duration does not decrease for a movement toward a small target following the delivery of a large odor in comparison to that following the delivery of a small odor. We suspect that it is the relationship between the motor representations elicited by the small and the large odors and the accuracy requirements dictated by the end goal, which may account for such a difference. To elaborate, the motor representation elicited by the small odor calls for a precise positioning of fingers upon the target object. Therefore, such an accurate demand might be responsible for the increase in reaching duration for movements performed toward the large target in the presence of a small odor. Conversely, when the large odor is presented, the less accurate demand associated to this motor representation might not be suitable to grasp a small object requiring a greater level of accuracy. This issue will be taken up again within the General discussion when comparing the present results with those obtained in a previous study regarding the effect of olfactory stimuli on the grasping component (Castiello et al. 2006).

The hypothesis that odors may increase the level of alertness, thus determining a faster reaching movement, was not confirmed. No significant differences were found when comparing trials in which the odor was present with trials in which the odor was absent. These findings are not in line with previous evidence showing that the delivery of an olfactory stimulus can elicit a generalized facilitation effect on sensorymotor performance (Millot et al. 2002). We suspect that this lack of an effect can be ascribed to the fact that the "odor" and "no-odor" trials were intermingled within the same block. This issue was tackled in Experiment 2.

#### **Experiment 2**

The aim of this experiment was to rule out the possibility that in Experiment 1 facilitatory effects were masked by the concurrent presentation of different types of trial within the same block. This is because the level of alertness reached during odor trials (SS, LL, LS, and SL condition) may carry over into no-odor trials (OL and OS condition). Therefore, in the present experiment participants performed the no-odor trials in a separate block to the trials in which an odor was delivered.

#### Materials and methods

#### Subjects

Twenty-three right-handed subjects (12 females and 11 males, mean age of 22 with SEM of  $\pm 2$  years) took part in this experiment. They had the same characteristics of the subjects who participated in Experiment 1.

#### Apparatus, procedure, and data analysis

Apparatus, procedure, and data analysis were similar in all aspects to those of Experiment 1 except that the 48 trials were included in 2 different blocks: "No-odor" and "Odor" blocks. In the No-odor block, a total of 16 trials were administered, 8 for each target size (i.e., OS and OL condition). In the Odor block a total of 32 trials were administered, 8 trials for each odor-target size combination (i.e., SS, LL, SL, and LS condition). Within both the No-odor and Odor 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 interblock interval of 2 min was administered.

#### **Results and discussion**

The analyses revealed that reaching duration was shorter when the object to be grasped was large than when it was small (large = 1514 ± 70 ms; small = 1597 ± 73 ms,  $t_{22}$  = -5.90, P < 0.001) (see Figure 3, top panel). As depicted in Figure 3 (top panel), reaching duration was longer for SL (black bars) than for LL trials (horizontal striped bars) (SL = 1504 ± 90 ms; LL = 1469 ± 83 ms,  $t_{22}$  = 2.98, P < 0.01). Similarly, reaching duration for LS (gray bars) was longer than for SS trials (vertically striped bars) (LS = 1575 ± 84 ms; SS = 1544 ± 84 ms,  $t_{22}$  = 2.36, P < 0.05) (see Figure 3, top panel). In general, these findings replicated those for Experiment 1. Further, as reported in Figure 3 (bottom panel), reaching duration was longer for the no-odor (white bars) than for the odor (black bars) trials (no odor = 1621 ± 58 ms; odor = 1523 ± 85 ms,  $t_{22}$  = 1.83, P < 0.05).

With respect to the effect of odor size, the results of Experiment 2 confirm those obtained in Experiment 1. Specifically, whereas the delivery of a small odor determined a change in reaching duration in the direction of the experimental hypothesis, the delivery of a large odor determined an increase rather than a decrease in reaching duration as our hypothesis would predict. We offer the same explanation provided for the similar results obtained in Experiment 1 for this.



**Figure 3** Mean reaching duration for OL (no odor–large target), SL (small odor–large target), LL (large odor–large target), OS (no odor–small target), LS (large odor–small target), and SS (small odor–small target) conditions in Experiment 2 (top panel). Mean reaching duration for "No-odor" (odorless air delivered before reaching for the target) and "Odor" (either "small" or "large" odor administered before reaching for the target) blocks in the Experiment 2 (bottom panel). Error bars indicate SEM. Asterisks indicate significant values. (Upper panel: \*\*\* P < 0.001; \*\* P < 0.05; \*P < 0.01; lower panel: \*P < 0.05).

In terms of alertness, it appears that the mere presence of an odor produces a generalized decrease in reaching duration. This result contrasts to the lack of an alertness effect found in Experiment 1. As hypothesized above, the manner in which the odor and no-odor trials were presented could account for the different results. In Experiment 1, in which odor and no-odor trials were presented within the same block, the level of alertness reached during the odor trials may have extended to the no-odor trials, therefore diminishing the effect. In Experiment 2, in which odor and no-odor trials were presented in separate blocks, such a carry over did not occur and then the alertness effect emerged. A point worth mentioning is that reaching duration was shorter for Experiment 1 than for Experiment 2 regardless of experimental condition (see Figure 2 and 3 top panel). We are unclear about the possible reasons behind such difference. However, considering the critical differences between the 2 experiments, 2 factors may have lead to changes in reaching duration. The first concerns the idiosyncratic characteristics

of the participants who took part in the 2 experiments. The second, perhaps more interesting, concerns the type of experimental design adopted for the 2 experiments (fully randomized vs. blocked). This latter issue opens to the question of how differences in experimental design may bring to differences in the duration of reach-to-grasp movements. A question, however, which is not at the core of the experimentation included in the present manuscript.

#### General 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 odor was different from the size of the visual target. Furthermore, when trials preceded by the delivery of an odor were administered separately from trials in which the odor was not delivered, the presence of an olfactory stimulus determined a facilitation effect, which was evident as a shortening in reaching duration.

#### The effect of odor size on reaching duration

In the present study, when the odor was associated with an object of a different size to the target, reaching duration increases. These findings are compatible with previous research investigating reach-to-grasp movements performed in the presence of task-irrelevant objects belonging to the same or different sensory modality as the target (e.g., Castiello 1996; Gentilucci et al. 1998; Patchay et al. 2003, 2006). Importantly, they extend previous results, which demonstrated a cross talk between visual and olfactory information during a grasping task (Castiello et al. 2006) to the other main component of prehension, that is, reaching.

In this respect, a relevant issue to consider is the level of coordination between the reaching and the grasping components (e.g., Jeannerod 1981) during prehension. 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 odor 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 object. 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 odor) to a movement directed toward a large target would not dramatically prevent the completion of a successful action.

It is of interest to compare the present findings with those from the comparative literature on peck autoshaping in pigeons (LaMon and Zeigler 1984; Allan and Zeigler 1994; Ploog and Zeigler 1996). (We thank an anonymous reviewer for suggesting this possible interpretation of our results). In a series of experiments, it was demonstrated that pigeons learn by autoshaping to consider a visual stimulus (i.e., a spotlighted key) as a signal which predicts the presentation of an object (i.e., a food pellet) (LaMon and Zeigler 1984; Allan and Zeigler 1994). Specifically, upon seeing the signal, pigeons exhibited a peck-to-gape movement, which was similar, in terms of kinematics (e.g., key-peck latency and gape aperture), to that associated with the size of the presented object. When the object was small, key-peck latency increased and gape aperture decreased, and vice versa. In other words, the features of the peck-to-gape movement triggered by the signal were related to the intrinsic properties (i.e., size) of the object associated with the signal (Ploog and Zeigler 1996). Whereas these findings on pigeons mirror those obtained for the influence of olfactory stimuli on the grasping component in humans (Castiello et al. 2006), they differ with respect to those obtained in the current study for the reaching component. However, an important aspect to consider is that whereas in pigeons only the visual modality has been tested, here it was an odor signaling a visual object. Therefore, it might be that it is the sensory nature of the signal, which accounts for the differences between pigeons and humans in terms of the relationship between object size and movement latency. Support for this hypothesis comes from human studies in which both the signal and the signaled object belong to the visual modality. In these circumstances, the results mirror exactly what has been reported for pigeons (for a review, see Castiello 1999).

It is now necessary to comment on the mechanisms through which the size information conveyed by the odor affects reaching for a visual object. 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 blueprint (Jordan and 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 and 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 odor, the motor plan elicited by the olfactory information does not need to be changed; as it happens when the odor is small and the visual stimulus is large. Conversely, when the reach duration established according to the odor cannot satisfy the prerequisites for acting successfully upon the visual stimulus,

a correction is applied; as it happens when the odor is large and the visual stimulus is small.

Recent neurophysiological and neuroimaging evidence may allow to speculate on the neural bases underlying the effects reported here. For instance, it has been demonstrated that the orbitofrontal cortex (OFC), which contains the secondary olfactory cortex involved in odor recognition (for a review, see Sobel et al. 2003), is linked via either direct or indirect connections with motor areas subtending the dynamic control of prehensile behavior (for a review, see Cavada et al. 2000). Of interest is that the neural circuit underlying visually guided reach-to-grasp movements including the intraparietal sulcus (IPs), the ventral and the dorsal premotor cortices (PMv; PMd), and the primary motor cortex (M1) modulates with respect to the level of accuracy called by a visual stimulus (for a review, see Castiello and Begliomini 2008). Therefore, on the basis of the present results, it cannot be excluded that such modulation in terms of accuracy may also occur on the basis of an olfactory stimulus.

#### The presence of the odor alerts reaching actions

Alertness in behavioral 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 the reaction time in simple tasks (responses to visual or auditory stimulation) significantly decreased in the ambient odor conditions compared with the no-odor condition. Thus, the reported facilitation effect on reaching duration-due to olfactory stimulation regardless of odor size—can be considered to be a new piece in the puzzle of odor-induced behavior. This result may signify that an odor 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 et al. 1999; Zahariev and MacKenzie 2007). For instance, faster movement times have been found when redundant auditory information was presented (Zahariev and 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.

# Conclusions

The present results suggest that olfactory information plays an important role for the planning and control of reaching movements. The fact that the size of olfactory information modulates arm reaching leads to 2 important considerations in terms of sensorimotor transformation. First, from a perceptual perspective, the representation evoked by the odor seems to contain structural information about the object. Second, from a motor perspective, the olfactory-triggered motor plan embodies specific and selective commands for reaching the "smelled" object, and it is fully manageable by the motor system. Further, another aspect of the present results is how the similarity between the visual and olfactory motor blueprints modulates reaching duration. In this respect, we have identified a chemosensory–visual binding for the control of action. We found that when olfactory/visual information trigger different motor plans interference emerges.

The present findings open to a number of unsolved questions. For instance, would the olfactory interference reported here extend to object properties other than its size? In this respect, we know from kinematic literature that when the to-be-grasped object is slippery or fragile, the reach duration lengths with respect to when it is rough or sturdy (Fikes et al. 1994; Savelsberg et al. 1996). Whether the texture-fragility information provided by an odor (associated with orange versus persimmon fruit) would lead to a similar pattern of results remains to be investigated. Although the present findings do not allow making conclusive inferences on the level of information details carried by an odor, it is plausible that the aforementioned mechanisms might also be involved for object characteristics that go beyond its size. In neural terms, the natural question is how do brain areas responsible for multisensory integration, such as the OFC, modulate their activity when information for action planning is provided through different modalities? And, how do multisensory integration sites "talk" with the neural circuits underlying grasping as to modulate motor output? Further research using functional imaging and neurophysiological techniques may have the potential to uncover the neural underpinnings for the effects reported here.

# Funding

University of Padua to U.C. and R.T (CPDA067991/06).

# Acknowledgements

We thank Dr Jonathan Daisley for useful comments on an early version of this manuscript.

# References

- Allan RW, Zeigler HP. 1994. Autoshaping the pigeon's gape response: acquisition and topography as a function of reinforcer type and magnitude. J Exp Anal Behav. 62:201–223.
- Barker S, Grayhem P, Koon J, Perkins J, Whalen A, Raudenbush B. 2003. Improved performance on clerical tasks associated with administration of peppermint odor. Percept Mot Skills. 97:1007–1010.
- Castiello U. 1996. Grasping a fruit: selection for action. J Exp Psychol Hum Percept Perform. 22:582–603.

- Castiello U. 1999. Mechanisms of selection for the control of hand action. Trends Cogn Sci. 3:264–271.
- Castiello U, Badcock DR, Bennett KM. 1999. Sudden and gradual presentation of distractor objects: differential interference effects. Exp Brain Res. 128:550–556.
- Castiello U, Begliomini C. Forthcoming 2008. The cortical control of visually guided grasping. Neuroscientist.
- Castiello U, Zucco GM, Parma V, Ansuini C, Tirindelli R. 2006. Cross-modal interactions between olfaction and vision when grasping. Chem Senses. 31:665–671.
- Cavada C, Compañy T, Tejedor J, Cruz-Rizzolo RJ, Reinoso-Suárez F. 2000. The anatomical connections of the macaque monkey orbitofrontal cortex. A review. Cereb Cortex. 10:220–242.
- Dember WN, Warm JS, Parasuraman R. 1995. Olfactory stimulation and sustained attention. In: Gilbert AN, editor. Compendium of olfactory research. Dubuque (IA): Kendall/Hunt. p. 39–46.
- Fikes TG, Klatsky RL, Lederman SJ. 1994. Effects of object texture on precontact movement time in human prehension. J Mot Behav. 26:325–332.
- Furr RM, Rosenthal R. 2003. Repeated-measures contrasts for "multiplepattern" hypotheses. Psychol Methods. 8:275–293.
- Gentilucci M, Castiello U, Corradini ML, Scarpa M, Umiltà C, Rizzolati G. 1991. Influence of different types of grasping on the transport component of prehension movements. Neuropsychologia. 29:361–378.
- Gentilucci M, Daprati E, Gangitano M. 1998. Haptic information differentially interferes with visual analysis in reaching-grasping control and in perceptual processes. Neuroreport. 9:887–891.
- Hummel T, Knecht M, Kobal G. 1996. Peripherally obtained electrophysiological responses to olfactory stimulation in man: electro-olfactograms exhibit a smaller degree of desensitization compared with subjective intensity estimates. Brain Res. 717:160–164.
- Jakobson LS, Goodale MA. 1991. Factors affecting higher-order movement planning: a kinematic analysis of human prehension. Exp Brain Res. 86:199–208.
- Jeannerod M. 1981. Specialized channels for cognitive responses. Cognition. 10:135–137.
- Jordan MI, Wolpert DM. 1999. Computational motor control. In Gazzaniga M, editor. The Cognitive Neurosciences. Cambridge (MA): MIT Press.
- Kawato M. 1999. Internal models for motor control and trajectory planning. Curr Opin Neurobiol. 9:718–727.
- Keppel B. 1982. Design and analysis: a researcher's handbook. Englewood Cliffs (NJ): Prentice Hall.
- LaMon BC, Zeigler HP. 1984. Grasping in the pigeon (*Columba livia*): stimulus control during conditioned and consummatory responses. Anim Learn Behav. 12:223–231.
- Marteniuk RG, MacKenzie CL, Jeannerod M, Athenes S, Dugas C. 1987. Constraints on human arm movement trajectories. Can J Psychol. 41: 365–378.
- Millot JL, Brand G, Morand N. 2002. Effects of ambient odors on reaction time in humans. Neurosci Lett. 322:79–82.
- Patchay S, Castiello U, Haggard P. 2003. A cross-modal interference effect in grasping objects. Psychon Bull Rev. 10:924–931.
- Patchay S, Haggard P, Castiello U. (2006) An object-centred reference frame for control of grasping: effects of grasping a distractor object on visuomotor control. Exp Brain Res. 170:532–542.

- Ploog BO, Zeigler HP. 1996. Effects of food-pellet size on rate, latency, and topography of autoshaped key pecks and gapes in pigeons. J Exp Anal Behav. 65:21–35.
- Savelsbergh GJP, Steenbergen B, van der Kamp J. 1996. The role of fragility information in the guidance of the precision grip. Hum Mov Sci. 15: 115–128.
- Sobel N, Johnson BN, Mainland J, Yousem DM. 2003. Functional neuroimaging of human olfaction. In: Doty RL, editor. Handbook of olfaction and gustation II. New York: Marcel Dekker. p. 263–266.
- Stevens JP. 2002. Applied multivariate statistics for the social sciences IV. Mahwah (NJ): Lawrence Erlbaum Associates.
- Thompson B. 1985. Alternate methods for analyzing data from experiments. J Exp Educ. 54:50–55.

- Tipper SP, Howard LA, Jackson SR. 1997. Selective reaching to grasp: evidence for distractor interference effects. Vis Cogn. 4:1–38.
- Warm JS, Dember WN, Parasuraman R. 1991. Effects of olfactory stimulation on performance and stress in a visual sustained attention task. J Soc Cosmet Chem. 42:199–210.
- Welsh T, Elliott D. 2004. Movement trajectories in the presence of a distracting stimulus: evidence for a response activation model of selective reaching. Q J Exp Psychol A. 57:1031–1057.
- Wolpert DM, Ghahramani Z. 2000. Computational principles of movement neuroscience. Nat Neurosci. 3:1212–1217.
- Zahariev MA, MacKenzie CL. 2007. Grasping at 'thin air': multimodal contact cues for reaching and grasping. Exp Brain Res. 180:69–84.
- Accepted February 18, 2008