

The Effects of Task-Irrelevant Olfactory Information on the Planning and the Execution of Reach-to-Grasp Movements

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Abstract Previous evidence indicates that, when reaching to grasp a target object, the presence of nontarget irrelevant information (i.e., distractor) presented either in the visual or olfactory modality determines significant interference effects on temporal parameters, such as reaction time and movement time, and on movement kinematics. While research on “visual” distractor 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 odor evoking either a small or a large object. When the type of grasp evoked by the odor 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 nontargets produced no interference effects on movement kinematics, but they did on key temporal measures, i.e., reaction time and reach duration. These findings are discussed in light of current theories put forward to explain the sensory processes underlying the control of action.

Keywords Kinematics · Motor Control · Olfaction · Reach-to-Grasp Movements · Reaction Time · Selection for Action

Introduction

A fundamental problem for those interested in sensorimotor integration to solve is how perceptual inputs are able to guide actions. The environments within which humans have evolved are very complex, containing many objects towards which action might be directed. Hence, because of evolutionary pressures to survive in complex environments, highly efficient mechanisms have been implemented to link action selectively with particular objects. By necessity, then, these mechanisms must represent more than the target object for action. For example, consider the apparently trivial task of reaching for a glass from a table containing other potentially graspable objects. Coherent action, in which the hand is accurately directed to the appropriate glass, would be very difficult if the remaining perceptual information were not fully represented. That is, other competing objects have to be represented as they, indirectly, guide the action to the target object. The hand can move around or over irrelevant objects only if they are represented to some extent.

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Compelling evidence that to-be-ignored objects are represented comes from a series of studies showing that selecting a target for grasping in the presence of a distractor object leads to interference effects on movement kinematics [see Castiello (1998) and Tipper et al. (1998) for review]. In these studies, distractor size has been identified as a key parameter for revealing such interference effects, for instance, asking participants to reach towards and grasp a visual target in the presence of distractor objects of different sizes from the target influenced fingers' shaping. Specifically, it was found that the participants' amplitude of peak grip aperture (i.e., the maximum distance reached by the index finger and the thumb during reaching) while en-route to the target was influenced by the size of the distractor (e.g., Castiello 1996). If the target was small, the amplitude of peak grip aperture was greater when the distractor was large than when no distractor was present. Conversely, the amplitude of peak grip aperture for the grasp of a large target was less when the distractor was small than when there was no distractor.

Recently, the same effects have been found within the multimodal domain by asking participants to act upon visual targets in the presence of distractors signaled through the proprioceptive and the auditory sensory modalities (Patchay et al. 2005; Castiello et al. 2007). The perspective of a motor control system susceptible to signals that flow through different sensory modalities has prompted the investigation of multimodal links also involving chemosensory modalities. This was a reasonable question to ask given that olfaction, as other modalities, has the ability to convey information that is relevant for interacting with objects (e.g., shape, size). In a series of studies (Castiello et al. 2006; Tubaldi et al. 2008a, b; see also Rossi et al. 2008), participants were requested to reach towards and grasp a small or a large visual target in the absence or in the presence of an odor evoking either a small or a large object. When the "size" of the object evoked by the odor did not coincide with that for the visual target, interference effects were evident on the kinematics of hand shaping. It was found that, when participants grasped a small target (i.e., a strawberry) in the presence of a "large" odor (i.e., orange odor), the fingers' extension was greater (showing similarity with the pattern of hand shaping elicited by the large target when grasped in the absence of olfactory information) with respect to when the small target was grasped in the absence of olfactory information. When participants grasped a large target (i.e., an orange) in the presence of a "small" odor (i.e., strawberry odor), the fingers' flexion was greater (showing similarity with the pattern of hand shaping elicited by the small target when grasped in the absence of olfactory information) with respect to when the large target was grasped in the absence of olfactory information. Furthermore, reach duration was longer for trials in which

the odor size and the visual target did not match than when they matched. These findings were taken as the evidence that olfactory representations of objects contain highly detailed "motoric" information able to elicit the planning for a reach-to-grasp movement suited to interact with the olfactory-evoked object.

Altogether, these results have been explained in terms of an initial perceptual analysis during which a limited number of objects potentially relevant for action are processed in parallel. This initial perceptual processing flows continuously into areas of the brain that represent and subsequently initiate action. Such perceptual inputs are capable of automatically activating their associated responses without participants' intentions to act (Lhermitte 1983). Due to this highly efficient and automatic conversion of perceptual inputs into the actions, different sensory inputs can evoke actions in parallel. As soon as the target is identified, an appropriate reach-to-grasp motor plan is initialized, which then competes with the motor plan triggered by the distractor. This conflict is played out in the kinematics of hand shaping, whose reorganization is a time-consuming process that leads to an increase in reach duration.

An important aspect to consider for the revelation of such interference effects, which so far has only been investigated when visual distractors are presented, is concerned with previous knowledge regarding the nature of the target. If participants did not know which object was the target, or most likely to be the target, before the action started, then interference emerged (e.g., Tipper et al. 1997). Conversely, if participants had previous knowledge regarding the target then interference effects were not evident (e.g., 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.

Here, we wanted to investigate whether the interfering effect that the size of an odor has on the execution of a reach-to-grasp movement, as previously demonstrated when participants did not know the nature of the to-be-grasped target before movement initiation (Castiello et al. 2006; Tubaldi et al. 2008a, b), fades away when the participants know in advance the nature of the visual target. If previous knowledge of the visual target allows for an efficient filtering of irrelevant olfactory information, then no effects on movement kinematics and reach 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.

Methods

Participants

Nine right-handed participants [four females and five males, mean age $21 \pm$ standard error (SE)=2 years] took part in the experiment. All participants reported normal olfaction, no history of olfactory dysfunction, and normal or corrected-to-normal vision in a confidential report. All participants were naïve as to the purpose of the experiment and gave their informed written consent to participate in the study. The experimental session lasted approximately 30 min. The experimental procedures were approved by the Institutional Review Board at the University of Padua and were in accordance with the declaration of Helsinki.

Apparatus and Materials

The visual stimuli (i.e., targets) consisted of four plastic objects grouped on the basis of their natural size: small (almond, strawberry) and large (apple, orange) (Fig. 1A). Plastic objects were used in order to maintain consistent visual attributes and sizes similar throughout the period of

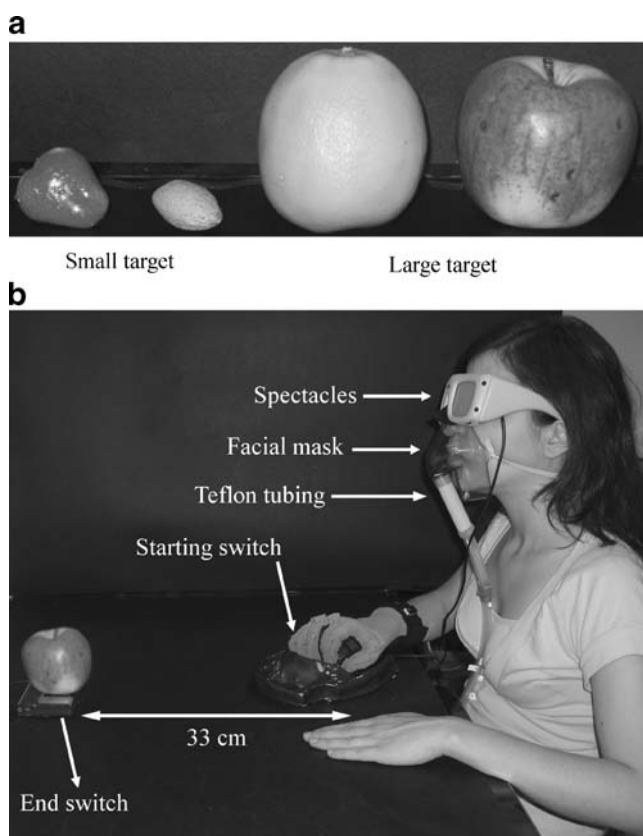


Fig. 1 **A** The small (i.e., an almond and a strawberry) and the large (i.e., an apple and an orange) stimuli used as visual targets in the present experiment. **B** The experimental set-up. The legends indicate the parts composing the experimental set up

experimentation. The odor stimuli corresponded to the target stimuli described above. Odor solutions of strawberry, almond, orange, and apple were obtained mixing 6,000 μ l of propylene glycol and 180 μ l (3%), 60 μ l (1%), 420 μ l (7%), and 45 μ l (0.75%) of the specific odorant compound, respectively. A custom-built computer-controlled olfactometer (Department of Experimental Psychology, University of Oxford) was used to deliver the odor stimuli. Each odor generator consisted of a glass boat containing one of the four odor stimuli. The air passed over the odor solutions and the propylene glycol at a flow rate of 8 l/min and it was delivered to subjects via Teflon tubing to a facial mask (Fig. 1B). In order to ensure that participants were able to identify each of the four delivered odors (i.e., orange odor, apple odor, strawberry odor, and almond odor), they performed an odor recognition task. Before experimentation started, participants were presented with the four visual objects (i.e., an orange, an apple, a strawberry, and an almond). Then, an odor was presented for 2 s and participants were instructed to indicate the object associated with the delivered odor. A total of eight trials (four for each type of odor) were presented in a randomized order. When performing the task, participants did not commit errors. Further, each odor was judged similarly in terms of intensity, hedonic tone, and familiarity. Altogether, these pre-experimentation procedures lasted 15 min. At the beginning of each trial, participants placed their right hand on a starting platform, within which a pressure sensitive switch was embedded (i.e., starting switch). The platform was designed with slight convexities dictating a natural flexed posture of the fingers (Fig. 1B). The target object was placed on a second pressure-sensitive switch (i.e., the ending switch) embedded within the working surface (Fig. 1B). Vision was controlled using spectacles fitted with liquid crystal lenses (Translucent Technologies, Toronto, Ontario, Canada) that rendered the target visually accessible by changing from opaque to clear (Fig. 1B).

Procedure

Participants began each trial with the elbow and the wrist resting on a flat surface, the forearm horizontal, the arm oriented in the parasagittal plane passing through the shoulder, and the right hand in a pronated position with the palm toward the working surface on the starting switch. The target was aligned with the participant's body midline and located at a 33-cm distance from the hand starting position to the left of the participant's right shoulder (Fig. 1B). The sequence of events for each trial was as follows: (1) vision was occluded before the target was positioned on the working surface; (2) an auditory tone (850 ms duration, 65 dB sound pressure, and 800 Hz

frequency) indicated odor delivery; (3) after 3 s, a similar tone indicated the offset of odor delivery; (4) the lenses of the spectacles were cleared. Following this event, participants decided when to start the action (i.e., reach towards, grasp, and lift the target object). Sufficient time (10 s) was allowed between trials to recover from any odor adaptation (Hummel et al. 1996). Participants were instructed not to grasp the object by the stem. Movement offset was taken at the time at which the ending switch was released when the object was lifted. The experimenter visually monitored each trial to ensure the participant's compliance to these requirements. Participants naturally grasp the small objects between the thumb and either (or both) the index and the middle fingers and the large objects opposing the thumb with all the other fingers.

This experimental task was performed under four different experimental conditions:

1. "Large odor–large target" condition: an odor associated with an object of a large size was presented before the reach-to-grasp movement towards a large target was initiated.
2. "Small odor–small target" condition: an odor associated with an object of a small size was presented before the reach-to-grasp movement towards a small target was initiated.
3. "Small odor–large target" condition: an odor associated with an object of a small size was presented before the reach-to-grasp movement towards a large target was initiated.
4. "Large odor–small target" condition: an odor associated with an object of a large size was presented before the reach-to-grasp movement towards a small target was initiated.

Participants performed a total of 32 trials (eight for each experimental condition), which were presented within one block and randomized within and across participants.

Recording Techniques

Hand posture was measured by resistive sensors embedded in a glove (CyberGlove, Virtual Technologies, Palo Alto, CA, USA) worn on the subject's right hand (Fig. 1B). The sensors' linearity was 0.62% of maximum nonlinearity over the full range of hand motion. The sensors' resolution was 0.5°, which remains constant over the entire range of joint motion. The output of the transducers was sampled at a 12-ms interval. Angular excursion was measured at metacarpal phalangeal (*mcp*) and proximal interphalangeal (*pip*) joints of the thumb, index, middle, ring, and little fingers. Abduction angles between the thumb–index, index–middle, middle–ring, and ring–little fingers were measured. Before the experimental block started, baseline

hand posture for each participant was recorded. Participants were requested to place their right hand flat on the table with the fingers straightened, close to each other and to hold that position until baseline fingers' angular excursion and abduction angles were recorded. Angular excursion and abduction angles were defined as 0° when the fingers were maintained straight and together in the plane of the palm ("reference hand posture"). Fingers' flexion was assigned positive values, whereas fingers' extension was given negative values with respect to the baseline. Abduction angles were reported on a continuum of positive values with respect to the baseline. An increase in such values indicated relatively greater abduction. Reach duration was calculated as the time interval between the release of the starting switch and the release of the ending switch upon which the target object rested. Reaction time was calculated as the time interval between the opening of the spectacles and the time the starting switch was released.

Data Analyses

To assess how the experimental conditions affected both reach duration and reaction time, two analyses of variance (ANOVAs) with odor size (large, small) and target size (large, small) as within-subjects factors were performed. Then, results from ANOVAs were explored by means of pair-wise comparisons. The effect of the experimental conditions on hand shaping was tested as follows: First, data from each trial performed by each participant were time-normalized. Specifically, the pattern for both digits' angular excursion and abduction angles was calculated from 10% to 100% of reach duration, at 10% intervals. Second, time-normalized data were averaged across trials within each individual according to the different experimental conditions. These averaged time-normalized data were subsequently entered into an ANOVA with odor size (large, small), target size (large, small), and time (from 10 to 100%, by step of 10%) as within-subjects factors. Greenhouse–Geisser correction was applied to the degrees of freedom of *F* statistics when the Mauchly test showed that the sphericity assumption was violated ($p < 0.05$).

Results

The odor size by target size interaction was significant for both reach duration [$F_{(1, 8)} = 11.76$, $\eta_p^2 = 0.595$, $p = 0.009$] and reaction time [$F_{(1, 8)} = 7.25$, $\eta_p^2 = 0.475$, $p = 0.027$]. For reach duration, when the target was large, post hoc analyses revealed that reach duration was longer when the size of the odor did not match the size of the target (i.e., small odor–large target condition) with respect to when the two sizes did match (i.e., large odor–large target condition) [$M =$

1,559 ms; SE=119 ms vs. $M=1,495$ ms; SE=119 ms, respectively, $t(8)=3.05$, $p=0.016$, see Fig. 2A]. In contrast, when the target was small, pair-wise comparisons showed that reach duration for the large odor–small target was similar to that observed for the small odor–small target condition [$M=1,547$ ms; SE=119 ms vs. $M=1,510$ ms; SE=108 ms, respectively, $t(8)=2.10$, $p=0.07$, see Fig. 2A]. For reaction time, when the target was large, there were no significant differences when comparing the small odor–large target with the large odor–large target condition [$M=540$ ms; SE=67 ms vs. $M=537$ ms; SE=54 ms, respectively, $t(8)=0.01$, $p=0.926$, see Fig. 2B]. Conversely, for a small target, reaction time was longer when the size of the odor did not match the size of the target (i.e., large odor–small target condition) with respect to when the two sizes did match (i.e., small odor–small target condition) [$M=592$ ms; SE=72 ms vs. $M=516$ ms; SE=64 ms, respectively, $t(8)=2.40$, $p=0.044$, see Fig. 2B]. With respect to measures related to hand shaping when the target was large and the odor was associated with a small object, only the ring–little abduction angle was smaller than that measured

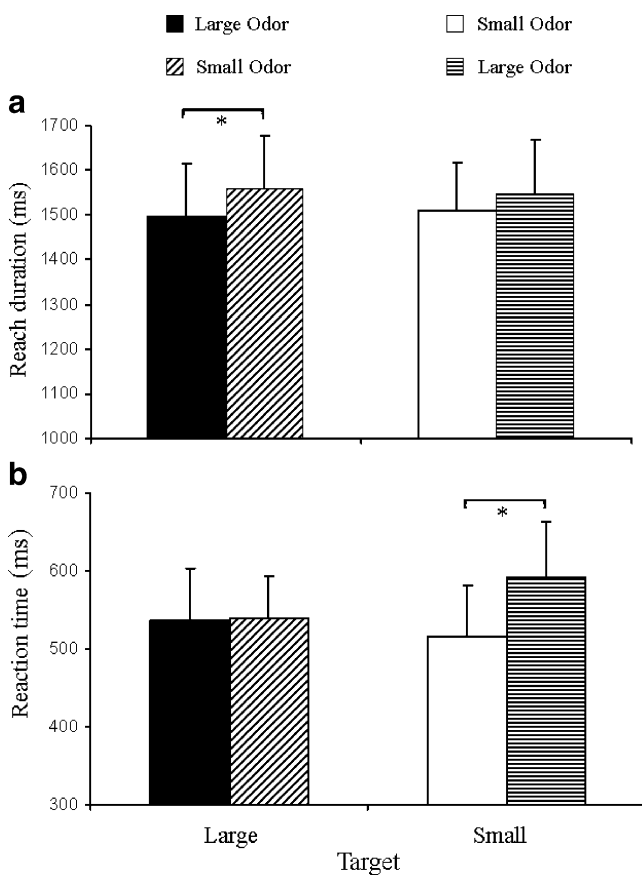


Fig. 2 The mean reach duration (A) and the mean reaction time (B) for each odor size and visual target size combination (i.e., small odor–large target, large odor–large target, large odor–small target, and small odor–small target). Error bars indicate mean SE. Asterisks indicate significant values ($p < 0.05$)

after smelling an odor associated with a large object [odor size by target size interaction, $F_{(1, 8)}=10.95$, $\eta_p^2=0.58$, $p=0.011$, see Fig. 3A]. This effect was particularly evident within the second half of reach duration (i.e., from 50% up to 100% of normalized reach duration) [interaction odor size by time, $F_{(2.06, 16.49)}=3.42$, $\eta_p^2=0.30$, $p=0.056$, see Fig. 3A]. When the target was small, the mismatch between the size of the odor and the size of the visual target did not significantly affect both fingers' angular excursion and abduction angles ($p_s > 0.05$; for an example, see Fig. 3B).

Discussion

We set out to investigate whether previous knowledge of the features characterizing a target object minimizes the interference effects that task-irrelevant 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 reach duration depending on the relationship between the size of the odor and the size of the visual target. When the size of the odor was small and

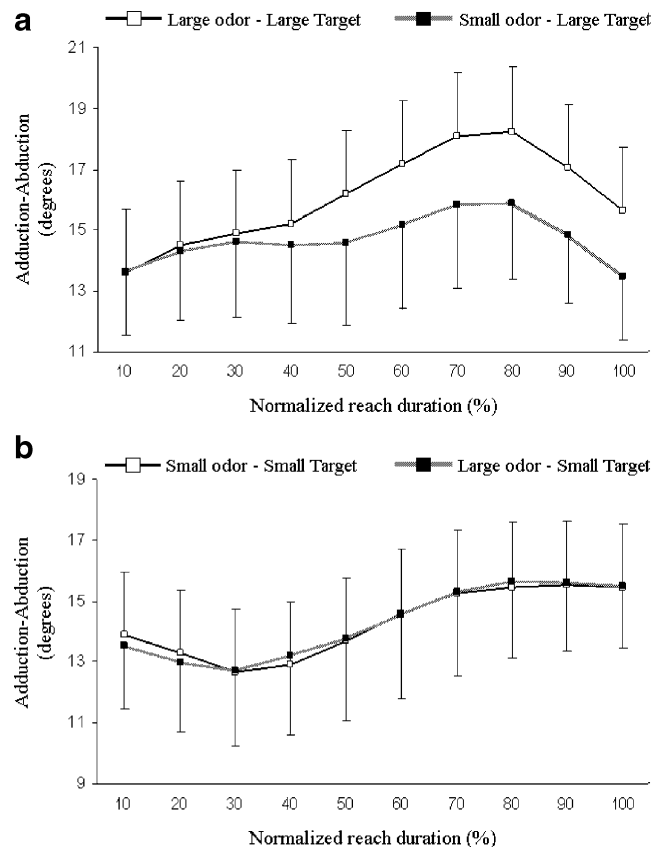


Fig. 3 Time course of abduction angle between ring and little fingers. Each trace corresponds to the time course of the average abduction angle for the large odor–large target and small odor–large target (A) and for the small odor–small target and the large odor–small target conditions (B). Error bars represent mean SE

the visual target was large, reach duration increased, but reaction time remained unchanged; when the size of the odor was large and the visual target was small, reaction time increased, but reach duration was unaltered. Further, effects due to the mismatch between the size of the odor and the size of the visual target were evident on an abduction angle only when the visual target was large.

Previous research concerning reaching and grasping has shown interference effects of nontargets presented in the visual modality disappeared on movement kinematics when nontarget objects were presented long before overt behavior began (e.g., Castiello 1996; Chieffi et al. 1993; Jackson et al. 1995; Tipper et al. 1997). Here, we extend this literature by demonstrating that, when nontargets are signaled 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 task-irrelevant information has to be filtered out. In the case of visual irrelevant 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 nontarget.

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 (e.g., Hick 1952). Abduction angles and reach duration are measures that reflect changes on movement execution when task-irrelevant information is presented (Ansuini et al. 2007; Meegan and Tipper 1998; Pratt and Abrams 1994; Tipper et al. 1992, 1997).

With this in mind, our preferred explanation for the present results is the following: When the delivered odor was “small” and the visual target was large, participants prepared the movement on the basis of the small odor, 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 odor considered a level of accuracy that could satisfy grasping for 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 hand. However, when grasping large objects by opposing the thumb to the forefingers, the last three fingers are extended farther from each other and from the palm of hand. Therefore, an adjustment might be necessary to revise biomechanical constraints. Indeed, the result for the abduction angle associated to the small odor–large target condition suggests that such adjustment occurs on-line, inducing the observed increase in reach duration.

When the delivered odor 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 onset and the target onset automatically trigger the planning of movements (Meegan and 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 irrelevant olfactory information, accuracy plays an important role in determining the time course of interference.

In conclusion, the present findings demonstrate that the interference effects dictated by olfactory irrelevant information might remain even when participants are given prior knowledge of the target object. This is intriguing because it suggests that visual feedback somehow does not reconfigure or “reset” motor responses to odor as it happens with irrelevant visual stimuli.

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