



## Research report

## Grasping a fruit. Hands do what flavour says

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## ABSTRACT

Previous research on multisensory integration during goal-directed natural actions reported that visual, proprioceptive, auditory and orthonasal olfactory stimulation has the ability to influence motor control. In this study, we used kinematics to investigate the integration between vision and flavour perception during reach-to-grasp movements. Participants were requested to drink a sip of flavoured solution and then grasp an object presented in central vision. The results indicate that when the objects evoked by the flavour and by the visual target were of a similar size (i.e., large or small) and evoked the same kind of hand shaping in order to be grasped (i.e., congruent condition) facilitation effects emerged. Conversely, when the object evoked by the flavour and by the visual target was of a different size and evoked a different kind of hand shaping in order to be grasped (i.e., incongruent condition) interference effects emerged. Interference effects, however, were only evident for the combination involving a large visual target and a 'small' flavour. When comparing hand kinematics between the congruent and a 'no flavour' condition (i.e., water), facilitation effects emerged in favour of the former condition. Taken together, these results indicate the contribution of complex chemosensory stimuli for the planning and execution of visually guided reach to grasp movements. And, contribute to the current debate regarding the multisensory nature of the sensorimotor transformations underlying motor performance.

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## Introduction

Humans are biologically equipped with a number of systems that allow for a successful interaction with their environment: a sensory system to perceive changes in the environment, a motor system to act on the environment and a cognitive system to make sense of the environment (Schiffstein & Hekkert, 2008). Most events in everyday life simultaneously involve these different systems which mutually interact to provide us with a coordinated and integrated view of our world (Guest, Catmur, Lloyd, & Spence, 2002; Lalanne & Lorenceau, 2004; Pouget, Deneve, & Duhamel, 2002; Schubotz, 2007; Stein & Meredith, 1990). Such coherent representation permits to solve environmental problems such as those concerned with planning goal-directed actions cued by different sensory inputs.

Recent research suggests that the motor system is influenced by information coming from different sensory modalities such as vision, proprioception, audition and olfaction (D'Ausilio, Altenmuller, Olivetti Belardinelli, & Lotze, 2006; Klatzky, Pai, & Krotkov, 2000; Patchay, Haggard, & Castiello, 2005; Tubaldi, Ansuini, Tirindelli, & Castiello, 2008). In some of these studies, visually

guided reach-to-grasp movements were preceded by the delivery of information presented in a different modality. Given that the appropriateness of hand shaping is directly proportional to the object dimension, with a slope estimated around 0.8 (Jeannerod, 1981), the differences in the parameterization of hand aperture largely depend upon the first-coming sensory modality. For instance, when a preceding orthonasally delivered olfactory information evokes the representation of an object similar in size to the visual target, then the aperture of the hand during reaching is more accurately sized than when the target is grasped in the absence of any preceding olfactory information. If the administered odour evokes an object of a different size than that evoked by the visual target, then hand coreography is less precise (Tubaldi et al., 2008). Having two modalities signalling target-motor-related properties determines either facilitation or interference effects depending on the congruency between preceding sensorial information and visual target information.

To our knowledge, no previous studies have investigated the effects that complex chemosensory stimuli, such as flavour, might have on motor control. Nevertheless, it is well known that flavour is bidirectionally tightly to a wide range of behaviours. It has been reported that flavour can influence memory (Mojet & Köster, 2002; Møller, Mojet, & Köster, 2007), attention (Levitan, Zampini, Li, & Spence, 2008), satiety (Yeomans, Leitch, Gould, & Mobini, 2008) and thirst reflex (Morley, Levine & Murray, 1981). As an example,

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in a study by Mojet and Köster (2002) participants were served with a kind of breakfast composed by different food targets. At a subsequent stage, they were unexpectedly asked to recognize the food they had eaten among slightly different distractors. The results showed that even minor changes in flavour (e.g., due to the use of different baking powders or grains) altered the participants' accuracy in recognizing the targets. This indicates that flavour information has the ability to modulate implicit learning.

As previously established, flavour is a complex combination of different sensory modalities, with taste and smell information playing a pivotal role in determining such multisensory experience (Auvray & Spence, 2008; Delwiche, 2004). Such combination has the potential to enrich (and influence) the multisensory experience of our environment in a number of daily actions, such as eating and drinking (Delwiche, 2004).

A large body of literature has already demonstrated that taste and smell are strictly connected sensory modalities. Dalton and colleagues (Dalton, Doolittle, Nagata, & Breslin, 2000) reported that when taste and smell stimuli are presented in subthreshold concentrations, a taste–smell interaction is present. Other research noticed that odour intensity judgments increase as taste compound concentration is increased, and vice versa, taste intensity judgments increase as odour compound concentration is increased, suggesting that taste–smell interactions are both odorant and tastant dependent (Frank & Byram, 1988). Moreover, the increased intensity judgment for both taste and olfactory stimuli is greater for congruent and typical taste–odour pairs (Schifferstein & Verlegh, 1996). Taken together, these data suggest that flavour is not resulting from the mere convergence of its sensory components, but it is “more than the sum of its parts” (Small, Jones-Gotman, Zatorre, Petrides & Evans, 1997).

Here we capitalize on these evidences to investigate whether the object representation evoked by flavour, is similar to that evoked by other sensorial stimuli in terms of motor-related properties. This is a reasonable question to ask given that indications of chemosensory–motor relations are already evident within the neurophysiological and the developmental literature. In first instance, Dinardo and Travers (1994) demonstrated that in rats gustatory stimulation activates the reticular formation in which are included pre-motor neurons responsible for the tongue and facial motor behaviours. These results lead to consider the possibility that the chemosensory information joins the motor nuclei via the reticular formation generating well-organized chemosensory-mediated motor actions. In second instance, Steiner (1973) demonstrated that both normocephalic, anencephalic and hydrocephalic newborns show the same facial expressions when stimulated by either a sweet or a bitter solution, suggesting that no superior cortical involvement is needed to determine flavour-guided motor behaviours.

The aim of the present study was to investigate whether central mechanisms for the visual guidance of motor behaviour are sensitive to complex chemosensory stimuli, such as flavour. We adopted a paradigm which has already been successful in revealing the effect of task irrelevant orthonasal olfactory information on the organization of visually guided reach-to-grasp movements (Castiello, Zucco, Parma, Ansuini & Tirindelli, 2006; Tubaldi et al., 2008). Nevertheless, the multimodal nature of the representations induced by retronasal stimulation raise an interesting question regarding whether flavour is able to modulate the motor control of the hand (Shepherd, 2006). Thus, we asked participants to reach towards and grasp a visually presented target following the delivery of a flavoured solution eliciting the representation of an object which can be congruent or incongruent with the visual target in terms of motor-related information. If flavour has the ability to elicit a motor plan related to the evoked object then this should be played out on movement kinematics in terms of hand

shaping. We expect that when the object evoked by flavour has similar structural features as the visual target then facilitation effects in terms of hand shaping appropriateness should be evident. Conversely when the object evoked by flavour has different structural features as the visual target then interference effects in terms of hand shaping appropriateness should be evident.

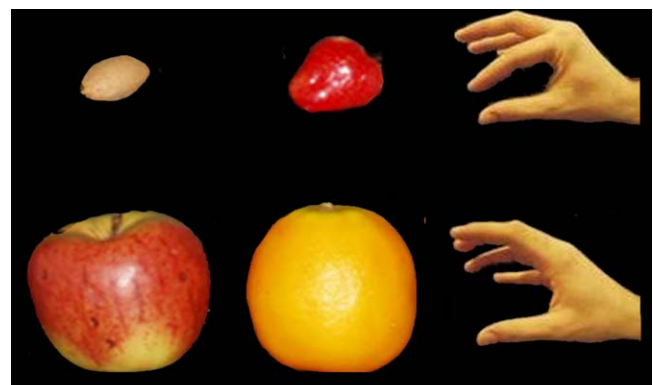
## Materials and methods

### Participants

Seventeen participants (12 women, 5 men; mean age = 25.1 - years, SD = 4.2 years) reporting normal smell and taste abilities, no history of smell and taste dysfunction, and normal or corrected-to-normal vision participated in the study. All were naïve as to the purpose of the experiment and gave their informed written consent to participate. 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.

### Stimuli

The visual stimuli (i.e., targets) consisted of four plastic objects grouped on the basis of their natural size: large (apple, orange) and small (almond, strawberry) and required different types of grasp: small objects needed a precision grip whereas large objects required a whole hand grip (Fig. 1, upper panel). Plastic objects were used in order to maintain consistent visual attributes and sizes throughout the period of experimentation. The flavour stimuli corresponded to the visual targets described above. Specifically, they consisted in 5 ml of either fruit juice (apple, orange, strawberry, water-diluted almond syrup) or water. A



Congruent Conditions		Incongruent Conditions		Control Conditions	
SS	LL	LS	SL	CS	CL

**Figure 1.** Upper panel shows the visual targets and the type of hand grasp they require. Almond and strawberry were defined as ‘small’ targets, whereas apple and orange were defined as ‘large’ targets. Lower panel represents flavour–visual target combination for the congruent, incongruent and control conditions.

custom-built apparatus was set to avoid participants smell the odours when delivering the flavour stimuli or water. The apparatus consisted in a set of 5 Teflon tubes (0.30 mm diameter). Each of them was connected to a computer-controlled 5-ml syringe filled-in with the solutions. At the time the flavour stimulation was delivered, the Teflon tube providing the to-be-administered solution was drawn up to the participant's mouth in order to favour the sipping.

### Procedure

The target was aligned with the participant's body midline and located at 33-cm distance from the hand starting position to the left of the subject's right shoulder. The sequence of events for each trial was as follows: (1) at the beginning of each trial participants were asked to eat a piece of water table cracker (1.5 g), to prevent taste adaptation; (2) to drink 10 ml of water as to remove food residuals; (3) to drink 5 ml of flavoured solution; (4) to close their eyes and keep them closed until the presentation of an auditory tone (frequency: 800 Hz; 500 ms duration), (5) which indicated participants to reach towards, grasp and lift the target object representing one of the aforementioned fruits. The experimenter visually monitored each trial to ensure subject's compliance to these requirements. A breach of instructions implicated the trial to be excluded from the final analyses. In order to evaluate how participants grasped the targets a pre-test session was executed. All the participants naturally grasped the small objects between the thumb and the index finger (i.e., precision grip) and the large objects opposing the thumb with all the other fingers (i.e., whole hand grasp). The experimental task was performed under six different experimental conditions (Fig. 1, lower panel): (i) congruent large (LL) in which both the flavour and the visual target evoked a large object (e.g., orange–apple), (ii) congruent small (SS) in which both the flavour and the visual target evoked a small object (e.g., strawberry–almond), (iii) incongruent large (LS) in which the flavoured solution evoked a large object but the visual target evoked a small object (e.g., orange–almond), (iv) incongruent small (SL) in which the flavoured solution evoked a small object and the visual target evoked a large object (e.g., strawberry–apple); (v) control large (CL) in which the flavour stimulus was water and the visual target evoked a large object (e.g., water–orange); and (vi) control small (CS) in which the flavour stimulus was water and the visual target evoked a small object (e.g., water–strawberry). Participants performed a total of 36 trials (6 for each experimental condition) which were presented in randomized order within three blocks.

### Apparatus

Movements were recorded by means of a three-dimensional motion analysis system (SMART-D, BTS) equipped with six-infrared-cameras (frequency 140 Hz) which picked up the reflectance of three passive markers (diameter = 0.25 cm) attached to (a) the wrist, (b) the tip of the index finger, and (c) the tip of the thumb of the participants' right hand. Markers were fastened using double-sided tape. Co-ordinates of the markers were reconstructed with an accuracy of 0.2 mm over the field of view. The standard deviation of the reconstruction error was 0.2 mm for the vertical (Y) axis and 0.3 mm for the two horizontal (X and Z) axes. Data were reconstructed, filtered (10 Hz) and analyzed with the SMART-D analyzer software.

### Dependent measures and statistical analyses

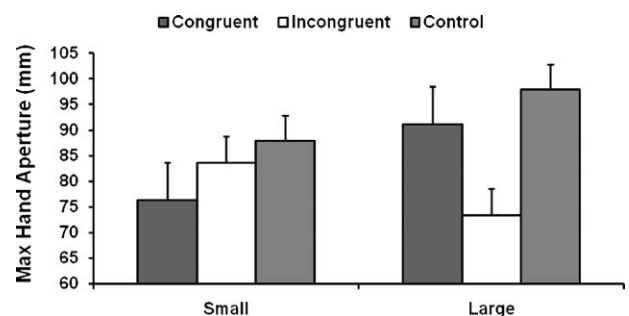
Kinematic analysis was confined to the amplitude and the time of maximum hand aperture, the most effective measures in

revealing how the planning and control of a visually guided prehensile movement is affected by irrelevant information presented in a different sensory modality (e.g., Castiello et al., 2006; Patchay et al., 2005). Maximum hand aperture was calculated as the distance in millimetres between the tip of thumb and the tip of the index finger, upon which the passive markers were positioned. The time of maximum hand aperture refers to the percentage of movement duration at which the maximum hand aperture occurred. Movement duration was calculated as the time between the release of wrist from the starting pad and the time at which the index finger and the thumb closed on the target and remained stationary for at least two frames (28 ms). Movement duration was normalized in order to obtain relative values (percentage) for the time of maximum hand aperture. A  $3 \times 2$  repeated-measures ANOVA with condition (congruent, incongruent, control) and target dimension (large, small) as within-subjects factors was performed on the dependent measures of interest. Bonferroni corrections ( $p < 0.05$ ) were applied when required.

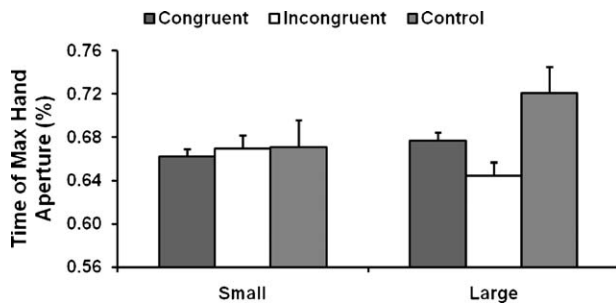
## Results

### Maximum hand aperture

When the visual target was grasped in the absence of preceding flavour information, maximum hand aperture was significantly greater for the larger than for the smaller targets (CL vs. CS: 100 mm vs. 88 mm, respectively;  $p < .0001$ ). Thus, the size of the visual target affected maximum hand aperture. This is a relevant finding since the present study aims at investigating the effects of flavour stimulation on maximum hand aperture. The 'condition by target size' interaction was also significant ( $F(2, 14) = 20.063$ ,  $p < .0001$ ,  $\eta_p^2 = .61$ ). As shown in Fig. 2, post hoc contrasts revealed that maximum hand aperture was more calibrated with respect to size when grasping for a large target was preceded by a sip of 'large' flavoured solution rather than by water (LL vs. CL: 92 mm vs. 100 mm,  $p < .001$ ). In a similar vein, maximum hand aperture was more adjusted to size when the small target was preceded by a 'small' fruit juice rather than by water (SS vs. CS: 75 mm vs. 88 mm,  $p < .01$ ). Conversely, grasping a large target following the delivery of a sip of 'small' fruit juice determined a maximum hand aperture which was smaller than when the same target was grasped following a sip of 'large' fruit juice (SL vs. LL: 74 mm vs. 92 mm,  $p < .0001$ ) or water (SL vs. CL: 74 mm vs. 100 mm,  $p < .0001$ ). When the action towards the small target started following a sip of 'large' rather than a 'small' fruit juice there was a tendency for maximum hand aperture to increase (LS vs. SS: 81 mm vs. 75 mm). Though, such difference was not



**Figure 2.** Schematic representation of the 'condition' by 'target size' interaction when considering the maximum hand aperture. The X axis shows the object sizes. Dark grey refers to congruent conditions, white to incongruent conditions and light grey to control conditions. Bars represent the standard error of means.



**Figure 3.** Schematic representation of the interaction 'condition' by 'target size' for the normalized time to maximum hand aperture. The X axis shows the object sizes. Dark grey refers to congruent conditions, white to incongruent conditions and light grey to control conditions. Bars represent the standard error of means.

significant. Similarly no difference in the amplitude of maximum hand aperture was found when a small target was grasped preceded by a sip of 'large' fruit juice or water (LS vs. CS: 81 vs. 88 mm).

#### *Time of maximum hand aperture*

The ANOVA revealed a significant 'condition' by 'target size' interaction ( $F(2, 14) = 7.25, p < .005, \eta_p^2 = .45$ ). Figure 3 shows that maximum hand aperture occurred earlier when a large target was preceded by a sip of juice evoking a large stimulus or water than when preceded by the delivery of a sip of 'small' fruit juice (LL vs. SL: 939 vs. 811 ms,  $p < .05$ ; CL vs. SL: 972 vs. 811 ms,  $p < .05$ ). When the small target was preceded by a sip of juice evoking a small object, a large object or water no significant differences were detected (see Fig. 3).

#### **Discussion**

In the present study, we have investigated the effects that flavour stimuli might have on the organization of visually guided reach-to-grasp movements. The present results confirm the classical effects of object dimension on grasping kinematics (e.g., Castiello, 2005) and indicate that when the 'size' of the flavour did match the size of the visual object facilitation effects emerged. In contrast, when the 'size' of the flavour did not match the size of the visual object interference effects arose, but only when the target was large. In other words, hand kinematics was modulated by the level of congruency between the visual- and the flavour-induced reach-to-grasp movement plans.

The present findings are in line with previous literature reporting on how different sensory modalities are used in concert to perceive and interact with multimodally specified objects and events. For example, crossmodal links between haptic information and visuomotor control have been reported in published experiments (Patchay, Castiello, & Haggard, 2003; Patchay et al., 2005). As found here, when the visual target and the task irrelevant stimulus differed in size, proprioceptively-guided manipulation of the task irrelevant stimulus influenced hand shaping. Specifically, the amplitude of maximum hand aperture was smaller, and the time to maximum hand aperture was earlier, when the object evoked by flavour was smaller than the target. Crossmodal action-perception effects have also been reported in studies that assessed the effects of orthonasally delivered olfactory information on visually guided reach-to-grasp movements (Castiello et al., 2006; Tubaldi et al., 2008). Participants reached towards and grasped either a small or a large visual target in the absence or in the presence of an odour evoking either a small or a large object. When the 'size' of the smell was congruent with

the visual size facilitation effects emerged in the kinematics of hand shaping. When the size of the 'smell' and that for the visual target were incongruent then interference effects emerged in the kinematics of hand shaping.

Here we extend the literature on the effects of multisensory processes underlying reach-to-grasp movements highlighting the potential role of a retronasally delivered complex sensory stimulus as flavour. We demonstrate for the first time that flavour has the ability to elicit motor plans which integrate or compete with those generated on the basis of the visual target.

A caveat of the present findings is that maximum hand aperture was not significantly increased for movements towards a small target following the delivery of a 'large' flavour in comparison to that following the delivery of a 'small' flavour. We suspect that it is the relationship between the motor representations elicited by the 'large' flavour and the accuracy requirements dictated by the end-goal (i.e., grasping a small visual target) which may account for such a difference. To elaborate, the motor representation elicited by the 'large' flavour poses less accurate demands in terms of movement. Therefore this motor representation might not be suitable to grasp a small target requiring a greater level of accuracy. This might be the reason why the system prevents the 'flavour' motor plan to kick in entirely, affect the amplitude and the timing of maximum hand aperture and prevent a successful grasp. A similar pattern of results was reported by Tubaldi and colleagues (2008) but not in a previous study (Castiello et al., 2006), in which orthonasal olfactory stimuli were delivered. These mixed findings might be explained in terms of the methodology used to deliver the olfactory stimulus. In the pioneering study by Castiello et al. (2006), the olfactory information was supplied by means of felt-tip pens impregnated with odour agents positioned under both nostrils for a period of 2 s. This kind of stimulation reduced the possibility of a prolonged olfactory exposition. In the second study (Tubaldi et al., 2008), the olfactory stimulation was provided via Teflon tubing to a facial mask and lasted approximately 3 s. In the present study the flavour stimulation was delivered via similar procedures. In these two latter studies, therefore, the exposition to the chemosensory stimulus was prolonged. Gaseous odours persisted within the mask (Tubaldi et al., 2008) and the solutions remained within the mouth because of the swallowing. In light of this it might be advanced that an extended olfactory stimulation, either orthonasal or retronasal, might provide sufficient time to reorganize the motor pattern avoiding interference. Support to this contention comes from the evidence of hand biomechanical constraints which naturally facilitate opening with respect to closing movements (Colebatch & Gandevia, 1989).

One might also hypothesize that the present results are exclusively due to retronasal olfactory information per se than by the multisensory nature of flavour. Although we cannot exclude such a possibility, we suggest that the facilitation effect arising when comparing the congruent with the control conditions might reflect a flavour multisensory process rather than an olfactory retronasal stimulation. Indeed, the comparison (congruent vs. control conditions) was not reported to be significant in previous studies when solely olfactory orthonasal stimulations were applied (e.g., Castiello et al., 2006). This might be in line with previous multisensory research reporting evidence of decrements in reaction times (e.g., Gottfried & Dolan, 2003) and increments in accuracy detection (Spence, Kettenmann, Kobal & McGlone, 2000; Spence, McGlone, Kettenmann & Kobal, 2001) in response to stimuli presented in different modalities. Support to this contention comes from a number of neuroimaging investigations providing evidence of either inhibition or activation in cortical chemosensory areas following olfactory orthonasal and retronasal stimulation, respectively (de Araujo, Rolls, Kringelbach, McGlone,

& Phillips, 2003; Small et al., 1997; Voss, Mak, Simmons, Parrish & Small, 2003).

The present findings indicate that flavour is able to elicit object representations involving motor properties. This might be surprising given that in real life situations at the time flavour is experienced the action towards the to-be-ingested food has already been terminated. However, as outlined above, literature from neurophysiological and developmental research reports some evidence of chemosensory–motor relations (Dinardo & Travers, 1994; Steiner, 1973). This evidence suggests that flavour perception, considered as the integration of taste, smell and visual inputs, roots in automatic, innate and low-level perceptual processing areas. Those areas relay to higher level areas, such as orbito-frontal cortex (OFC) (de Araujo et al., 2003), which is known to be involved in multisystem representations including flavour (Shepherd, 2006; Small, Bender, Veldhuizen, Rudenga, Nachtigal & Felsted, 2007; Rolls, 2001).

In this respect, it might be argued that the effects found in the present study are mediated by visual–flavour representations encoded at the level of multisensory integration sites within the OFC. But, how do these visual–flavour representations manage to modulate motor output? Comparative literature may provide some evidence for neural networks which connect the OFC with motor regions (Cavada, 2000). Of particular interest for our study is the presence of direct connections between OFC and motor areas involved in arm–hand movement control such as the motor cingulate area 24c/M3, the supplementary motor area F3/M2, the pre-supplementary motor area F6 and the ventral pre-motor area F5. Furthermore, also the primary motor cortex (M1) receives inputs from frontal granular area 12 (Morecraft & van Hoesen, 1993). On the basis of the well-known homology between cerebral regions underlying reach-to-grasp movement in monkeys and humans (Begliomini, Caria, Grodd, & Castiello, 2007; Castiello, 2005), we suggest that the cortico-cortical connections between OFC and motor areas influencing motor output in non human primates (Bates & Goldman-Rakic, 1993) may also exist in humans and account for the influence of multisensory information on motor behaviour and more specifically on prehensile actions.

At this stage it is tempting (and rather speculatively) to explain the results from the present study in light of survival mechanisms. At a first glance it might seem paradoxical that the common experiences of food selection, eating and drinking integrate information from more senses than do other perceptual experiences. However, the very fact that most of the organic substances – both nutritional and not – can be chewed and swallowed account for a change of perspective. According to this view, it might not be surprising that complex mechanisms have evolved to prevent food selection errors resulting in the ingestion of harmful compounds. Furthermore, if danger has to be avoided, sensory information should lead to rapid motor reaction to ensure a rapid rejection in order not to let the 'poison' enter the organism. Individually, each of the senses provides fundamental information to guide behaviour. But, the combined sensory input responsible for the flavour of foods underpins behaviours that maintain the basic structure and function of an organism (Stillman, 2002). From this perspective, creating and storing in memory exhaustive and redundant representations of objects, also involving flavoured–elicited motor plans, might be considered a helpful way to avoid needless risks (i.e., poisoning) when performing vital activities, such as eating or drinking.

## References

Auvray, M., & Spence, C. (2008). The multisensory perception of flavor. *Consciousness and Cognition*, 17(3), 1016–1031.

- Bates, J. F., & Goldman-Rakic, P. S. (1993). Prefrontal connections of medial motor areas in the rhesus monkey. *The Journal of Comparative Neurology*, 336(2), 211–228.
- Begliomini, C., Caria, A., Grodd, W., & Castiello, U. (2007). Comparing natural and constrained movements: new insights into the visuomotor control of grasping. *PLoS One*, 2(10), e1108.
- Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews*, 6, 726–736.
- Castiello, U., Zucco, G. M., Parma, V., Ansuini, C., & Tirindelli, R. (2006). Cross-modal interactions between olfaction and vision when grasping. *Chemical Senses*, 31(7), 665.
- Cavada, C. (2000). The anatomical connections of the macaque monkey orbitofrontal cortex. A review. *Cerebral Cortex*, 10(3), 220.
- Colebatch, J. G., & Gandevia, S. C. (1989). The distribution of muscular weakness in upper motor neuron lesions affecting the arm. *Brain*, 112(3), 749–763.
- D'Ausilio, A., Altenmuller, E., Olivetti Belardinelli, M., & Lotze, M. (2006). Cross-modal plasticity of the motor cortex while listening to a rehearsed musical piece. *European Journal of Neuroscience*, 24(3), 955–958.
- Dalton, P., Doolittle, N., Nagata, H., & Breslin, P. A. (2000). The merging of the senses: integration of subthreshold taste and smell. *Nature Neuroscience*, 3, 431–432.
- de Araujo, I. E. T., Rolls, E. T., Kringelbach, M. L., McGlone, F., & Phillips, N. (2003). Taste-olfactory convergence, and the representation of the pleasantness of flavour, in the human brain. *European Journal of Neuroscience*, 18(7), 2059–2068.
- Delwiche, J. (2004). The impact of perceptual interactions on perceived flavor. *Food Quality and Preference*, 15(2), 137–146.
- Dinardo, L. A., & Travers, J. B. (1994). Hypoglossal neural activity during ingestion and rejection in the awake rat. *Journal of Neurophysiology*, 72(3), 1181.
- Frank, R. A., & Byram, J. (1988). Taste–smell interactions are tastant and odorant dependent. *Chemical Senses*, 13(3), 445.
- Gottfried, J. A., & Dolan, R. J. (2003). The nose smells what the eye sees: crossmodal visual facilitation of human olfactory perception. *Neuron*, 39(2), 375–396.
- Guest, S., Catmur, C., Lloyd, D., & Spence, C. (2002). Audiotactile interactions in roughness perception. *Experimental Brain Research*, 146(2), 161–171.
- Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In J. Long & A. Baddeley (Eds.), *Attention and performance IX* (pp. 153–168). Hillsdale, NJ: Erlbaum.
- Klatzky, R. L., Pai, D. K., & Krotkov, E. P. (2000). Perception of material from contact sounds. *Presence: Teleoperators and Virtual Environments*, 9(4), 399–410.
- Lalanne, C., & Lorenceau, J. (2004). Crossmodal integration for perception and action. *Journal of Physiology – Paris*, 98(1–3), 265–279.
- Levitan, C. A., Zampini, M., Li, R., & Spence, C. (2008). Assessing the role of color cues and people's beliefs about color–flavor associations on the discrimination of the flavor of sugar-coated chocolates. *Chemosensory Perception*, 2(2), 53–58.
- Mojet, J., & Köster, E. P. (2002). Texture and flavour memory in foods: an incidental learning experiment. *Appetite*, 38(2), 110–117.
- Møller, P., Mojet, J., & Köster, E. P. (2007). Incidental and intentional flavor memory in young and older subjects. *Chemical Senses*, 32(6), 557–567.
- Morecraft, R. J., & van Hoesen, G. W. (1993). Frontal granular cortex input to the cingulate (M3), supplementary (M2) and primary (M1) motor cortices in the rhesus monkey. *The Journal of Comparative Neurology*, 337(4), 669–689.
- Morley, J. E., Levine, A. S., & Murray, S. S. (1981). Flavour modulates the antidipsogenic effect of substance P. *Brain Research*, 226(1–2), 334–338.
- Patchay, S., Castiello, U., & Haggard, P. (2003). A cross-modal interference effect in grasping objects. *Psychonomic Bulletin and Review*, 10(4), 924–931.
- Patchay, S., Haggard, P., & Castiello, U. (2005). Cross-modal links in action: evidence for an object-centred reference frame for control of grasping. *Experimental Brain Research*, 23, 1–11.
- Pouget, A., Deneve, S., & Duhamel, J. R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nature Reviews Neuroscience*, 3(9), 741–747.
- Rolls, E. T. (2001). The rules of formation of the olfactory representations found in the orbitofrontal cortex, olfactory areas in primates. *Chemical Senses*, 26(5), 595–604.
- Schiffman, H. N. J., & Hekkert, P. (2008). *Product experience*. Amsterdam: Elsevier.
- Schiffman, H. N. J., & Verlegh, P. W. J. (1996). The role of congruency and pleasantness in odor-induced taste enhancement. *Acta Psychologica*, 94(1), 87–105.
- Schubotz, R. I. (2007). Prediction of external events with our motor system: towards a new framework. *Trends in Cognitive Sciences*, 11(5), 211–218.
- Shepherd, G. M. (2006). Smell images and the flavor system in the human brain. *Nature*, 444(16), 316–321.
- Small, D. M., Bender, G., Veldhuizen, M. G., Rudenga, K., Nachtigal, D., & Felsted, J. (2007). The role of the human orbitofrontal cortex in taste and flavor processing. *Annals of the New York Academy of Sciences*, 1121, 136–151.
- Small, D. M., Jones-Gotman, M., Zatorre, R. J., Petrides, M., & Evans, A. C. (1997). Flavor processing: more than the sum of its parts. *Neuroreport*, 8(18), 3913–3917.
- Spence, C. B., Kettenmann, B., Kopal, G., & McGlone, F. P. (2000). Selective attention to the chemosensory modality. *Perception and Psychophysics*, 62, 1265–1271.
- Spence, C. B., McGlone, F. P., Kettenmann, B., & Kopal, G. (2001). Attention to olfaction. A psychophysical investigation. *Experimental Brain Research*, 138, 432–437.
- Stein, B. E., & Meredith, M. A. (1990). Multisensory integration: neural and behavioral solutions for dealing with stimuli from different sensory modalities. *Annals of the New York Academy of Sciences*, 608, 51–70.

- Steiner, J. E. (1973). The gustofacial response: observation on normal and anencephalic newborn infants. *Paper presented at the 4th symposium on oral sensation and perception*.
- Stillman, J. A. (2002). Gustation: intersensory experience par excellence. *Perception*, 31(12), 1491–1500.
- Tubaldi, F., Ansuini, C., Tirindelli, R., & Castiello, U. (2008). The grasping side of odours. *PloS One* 3(3).
- Voss, J., Mak, E., Simmons, K., Parrish, T. P., & Small, D. M. (2003). Neural correlates of chemosensory integration in humans studied with fMRI. *Chemical Senses*, 28, 554.
- Yeomans, M. R., Leitch, M., Gould, N. J., & Mobini, S. (2008). Differential hedonic, sensory and behavioral changes associated with flavor–nutrient and flavor–flavor learning. *Physiology and Behavior*, 93(4–5), 798–806.