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1 Research report

3 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

9 Humans are biologically equipped with a number of systems
10 that allow for a successful interaction with their environment: a
11 sensory system to perceive changes in the environment, a motor
12 system to act on the environment and a cognitive system to make
13 sense of the environment (Schiffstein & Hekkert, 2008). Most
14 events in everyday life simultaneously involve these different
15 systems which mutually interact to provide us with a coordinated
16 and integrated view of our world (Guest, Catmur, Lloyd, & Spence,
17 2002; Lalanne & Lorenceau, 2004; Pouget, Deneve, & Duhamel,
18 2002; Schubotz, 2007; Stein & Meredith, 1990). Such coherent
19 representation permits to solve environmental problems such as
20 those concerned with planning goal-directed actions cued by
21 different sensory inputs.

22 Recent research suggests that the motor system is influenced by
23 information coming from different sensory modalities such as
24 vision, proprioception, audition and olfaction (D'Ausilio, Alten-
25 muller, Olivetti Belardinelli, & Lotze, 2006; Klatzky, Pai, & Krotkov,
26 2000; Patchay, Haggard, & Castiello, 2005; Tubaldi, Ansuini,
27 Tirindelli, & Castiello, 2008). In some of these studies, visually
28 guided reach-to-grasp movements were preceded by the delivery

of information presented in a different modality. Given that the 29
appropriateness of hand shaping is directly proportional to the 30
object dimension, with a slope estimated around 0.8 (Jeannerod, 31
1981), the differences in the parameterization of hand aperture 32
largely depend upon the first-coming sensory modality. For 33
instance, when a preceding orthonasally delivered olfactory 34
information evokes the representation of an object similar in size 35
to the visual target, then the aperture of the hand during reaching 36
is more accurately sized than when the target is grasped in the 37
absence of any preceding olfactory information. If the adminis- 38
tered odour evokes an object of a different size than that evoked 39
by the visual target, then hand coreography is less precise (Tubaldi 40
et al., 2008). Having two modalities signalling target–motor- 41
related properties determines either facilitation or interference 42
effects depending on the congruency between preceding sensorial 43
information and visual target information. 44

45 To our knowledge, no previous studies have investigated the 46
effects that complex chemosensory stimuli, such as flavour, might 47
have on motor control. Nevertheless, it is well known that flavour 48
is bidirectionally tighted to a wide range of behaviours. It has been 49
reported that flavour can influence memory (Mojet & Köster, 2002; 50
Møller, Mojet, & Köster, 2007), attention (Levitan, Zampini, Li, & 51
Spence, 2008), satiety (Yeomans, Leitch, Gould, & Mobini, 2008) 52
and thirst reflex (Morley, Levine & Murray, 1981). As an example, 53
in a study by Mojet and Köster (2002) participants were served 54
with a kind of breakfast composed by different food targets. At a

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55 subsequent stage, they were unexpectedly asked to recognize the
 56 food they had eaten among slightly different distractors. The
 57 results showed that even minor changes in flavour (e.g., due to the
 58 use of different baking powders or grains) altered the participants’
 59 accuracy in recognizing the targets. This indicates that flavour
 60 information has the ability to modulate implicit learning.

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

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

84 Here we capitalize on these evidences to investigate whether
 85 the object representation evoked by flavour, is similar to that
 86 evoked by other sensorial stimuli in terms of motor-related
 87 properties. This is a reasonable question to ask given that
 88 indications of chemosensory–motor relations are already evident
 89 within the neurophysiological and the developmental literature. In
 90 first instance, Dinardo and Travers (1994) demonstrated that in
 91 rats gustatory stimulation activates the reticular formation in
 92 which are included pre-motor neurons responsible for the tongue
 93 and facial motor behaviours. These results lead to consider the
 94 possibility that the chemosensory information joins the motor
 95 nuclei via the reticular formation generating well-organized
 96 chemosensory-mediated motor actions. In second instance, Steiner
 97 (1973) demonstrated that both normocephalic, anencephalic and
 98 hydrocephalic newborns show the same facial expressions when
 99 stimulated by either a sweet or a bitter solution, suggesting that no
 100 superior cortical involvement is needed to determine flavour-
 101 guided motor behaviours.

102 The aim of the present study was to investigate whether central
 103 mechanisms for the visual guidance of motor behaviour are
 104 sensitive to complex chemosensory stimuli, such as flavour. We
 105 adopted a paradigm which has already been successful in revealing
 106 the effect of task irrelevant orthonasal olfactory information on the
 107 organization of visually guided reach-to-grasp movements (Cas-
 108 tiello, Zucco, Parma, Ansuini & Tirindelli, 2006; Tubaldi et al.,
 109 2008). Nevertheless, the multimodal nature of the representations
 110 induced by retronasal stimulation raise an interesting question
 111 regarding whether flavour is able to modulate the motor control of
 112 the hand (Shepherd, 2006). Thus, we asked participants to reach
 113 towards and grasp a visually presented target following the
 114 delivery of a flavoured solution eliciting the representation of an
 115 object which can be congruent or incongruent with the visual
 116 target in terms of motor-related information. If flavour has the
 117 ability to elicit a motor plan related to the evoked object then this
 118 should be played out on movement kinematics in terms of hand
 119 shaping. We expect that when the object evoked by flavour has
 120 similar structural features as the visual target then facilitation

effects in terms of hand shaping appropriateness should be 121
 evident. Conversely when the object evoked by flavour has 122
 different structural features as the visual target then interference 123
 effects in terms of hand shaping appropriateness should be 124
 evident. 125

Materials and methods 126

Participants 127

Seventeen participants (12 women, 5 men; mean age = 25.1 y 128
 ears, SD = 4.2 years) reporting normal smell and taste abilities, no 129
 history of smell and taste dysfunction, and normal or corrected-to- 130
 normal vision participated in the study. All were naïve as to the 131
 purpose of the experiment and gave their informed written 132
 consent to participate. The experimental session lasted approxi- 133
 mately 30 min. The experimental procedures were approved by 134
 the Institutional Review Board at the University of Padua and were 135
 in accordance with the declaration of Helsinki. 136

Stimuli 137

The visual stimuli (i.e., targets) consisted of four plastic objects 138
 grouped on the basis of their natural size: large (apple, orange) and 139
 small (almond, strawberry) and required different types of grasp: 140
 small objects needed a precision grip whereas large objects 141
 required a whole hand grip (Fig. 1, upper panel). Plastic objects 142
 were used in order to maintain consistent visual attributes and 143
 sizes throughout the period of experimentation. The flavour 144
 stimuli corresponded to the visual targets described above. 145
 Specifically, they consisted in 5 ml of either fruit juice (apple, 146
 orange, strawberry, water-diluted almond syrup) or water. A 147
 custom-built apparatus was set to avoid participants smell the 148
 odours when delivering the flavour stimuli or water. The apparatus 149



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, and to the right whereas apple and orange were defined as ‘large’ targets. Lower panel represents flavour–visual target combination for the congruent, incongruent and control conditions.

150 consisted in a set of 5 Teflon tubes (0.30 mm diameter). Each of
151 them was connected to a computer-controlled 5-ml syringe filled-
152 in with the solutions. At the time the flavour stimulation was
153 delivered, the Teflon tube providing the to-be-administered
154 solution was drawn up to the participant's mouth in order to
155 favour the sipping.

156 Procedure

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

192 Apparatus

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

205 Dependent measures and statistical analyses

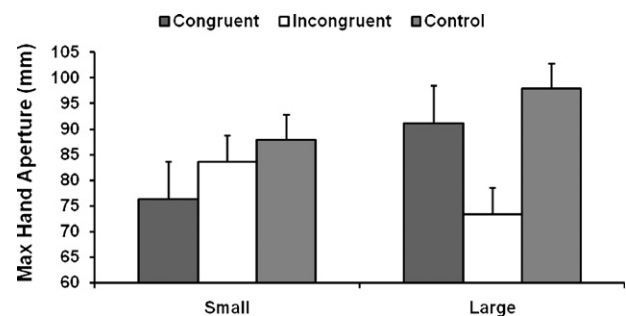
206 Kinematic analysis was confined to the amplitude and the time
207 of maximum hand aperture, the most effective measures in
208 revealing how the planning and control of a visually guided
209 prehensile movement is affected by irrelevant information

presented in a different sensory modality (e.g., Castiello et al., 210
2006; Patchay et al., 2005). Maximum hand aperture was 211
calculated as the distance in millimetres between the tip of 212
thumb and the tip of the index finger, upon which the passive 213
markers were positioned. The time of maximum hand aperture 214
refers to the percentage of movement duration at which the 215
maximum hand aperture occurred. Movement duration was 216
calculated as the time between the release of wrist from the 217
starting pad and the time at which the index finger and the thumb 218
closed on the target and remained stationary for at least two 219
frames (28 ms). Movement duration was normalized in order to 220
obtain relative values (percentage) for the time of maximum hand 221
aperture. A 3×2 repeated-measures ANOVA with condition 222
(congruent, incongruent, control) and target dimension (large, 223
small) as within-subjects factors was performed on the dependent 224
measures of interest. Bonferroni corrections ($p < 0.05$) were 225
applied when required. 226

227 Results

228 Maximum hand aperture

229 When the visual target was grasped in the absence of preceding 229
flavour information, maximum hand aperture was significantly 230
greater for the larger than for the smaller targets (CL vs. CS: 231
100 mm vs. 88 mm, respectively; $p < .0001$). Thus, the size of the 232
visual target affected maximum hand aperture. This is a relevant 233
finding since the present study aims at investigating the effects of 234
flavour stimulation on maximum hand aperture. The 'condition by 235
target size' interaction was also significant ($F(2, 14) = 20.063$, 236
 $p < .0001$, $\eta_p^2 = .61$). As shown in Fig. 2, post hoc contrasts revealed 237
that maximum hand aperture was more calibrated with respect to 238
size when grasping for a large target was preceded by a sip of 'large' 239
flavoured solution rather than by water (LL vs. CL: 92 mm vs. 240
100 mm, $p < .001$). In a similar vein, maximum hand aperture was 241
more adjusted to size when the small target was preceded by a 242
'small' fruit juice rather than by water (SS vs. CS: 75 mm vs. 88 mm, 243
 $p < .01$). Conversely, grasping a large target following the delivery 244
of a sip of 'small' fruit juice determined a maximum hand aperture 245
which was smaller than when the same target was grasped 246
following a sip of 'large' fruit juice (SL vs. LL: 74 mm vs. 92 mm, 247
 $p < .0001$) or water (SL vs. CL: 74 mm vs. 100 mm, $p < .0001$). 248
When the action towards the small target started following a sip of 249
'large' rather than a 'small' fruit juice there was a tendency for 250
maximum hand aperture to increase (LS vs. SS: 81 mm vs. 75 mm). 251
Though, such difference was not significant. Similarly no difference 252
in the amplitude of maximum hand aperture was found when a 253
small target was grasped preceded by a sip of 'large' fruit juice or 254
water (LS vs. CS: 81 vs. 88 mm). 255



256 **Figure 2.** Schematic representation of the 'condition' by 'target size' interaction 257
when considering the maximum hand aperture. The X axis shows the object sizes. 258
Dark grey refers to congruent conditions, white to incongruent conditions and light 259
grey to control conditions. Bars represent the standard error of means.

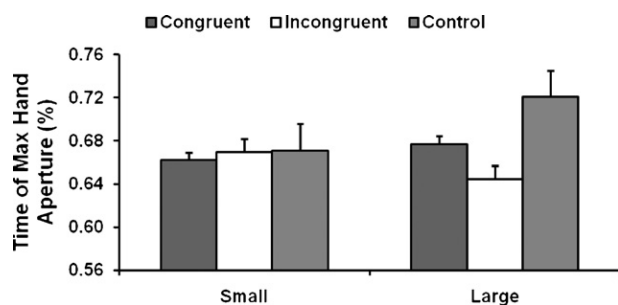


Figure 3. Schematic representation of the interaction 'condition' by 'target size' for the normalized time to maximum hand aperture. The X axis shows the object sizes. Dark grey refers to congruent conditions, white to incongruent conditions and light grey to control conditions. Bars represent the standard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

256 Time of maximum hand aperture

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

266 Discussion

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

278 The present findings are in line with previous literature
279 reporting on how different sensory modalities are used in concert
280 to perceive and interact with multimodally specified objects and
281 events. For example, crossmodal links between haptic information
282 and visuomotor control have been reported in published experi-
283 ments (Patchay, Castiello, & Haggard, 2003; Patchay et al., 2005).
284 As found here, when the visual target and the task irrelevant
285 stimulus differed in size, proprioceptively-guided manipulation of
286 the task irrelevant stimulus influenced hand shaping. Specifically,
287 the amplitude of maximum hand aperture was smaller, and the
288 time to maximum hand aperture was earlier, when the object
289 evoked by flavour was smaller than the target. Crossmodal action-
290 perception effects have also been reported in studies that assessed
291 the effects of orthonasally delivered olfactory information on
292 visually guided reach-to-grasp movements (Castiello et al., 2006;
293 Tubaldi et al., 2008). Participants reached towards and grasped
294 either a small or a large visual target in the absence or in the
295 presence of an odour evoking either a small or a large object. When
296 the 'size' of the smell was congruent with the visual size facilitation
297 effects emerged in the kinematics of hand shaping. When the size
298 of the 'smell' and that for the visual target were incongruent then
299 interference effects emerged in the kinematics of hand shaping.

300 Here we extend the literature on the effects of multisensory
301 processes underlying reach-to-grasp movements highlighting the
302 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 conten-
tion 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

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369 some evidence of chemosensory–motor relations (Dinardo &
370 Travers, 1994; Steiner, 1973). This evidence suggests that flavour
371 perception, considered as the integration of taste, smell and visual
372 inputs, roots in automatic, innate and low-level perceptual
373 processing areas. Those areas relay to higher level areas, such as
374 orbito-frontal cortex (OFC) (de Araujo et al., 2003), which is known
375 to be involved in multisystem representations including flavour
376 (Shepherd, 2006; Small, Bender, Veldhuizen, Rudenga, Nachtigal &
377 Felsted, 2007; Rolls, 2001).

378 In this respect, it might be argued that the effects found in the
379 present study are mediated by visual–flavour representations
380 encoded at the level of multisensory integration sites within the
381 OFC. But, how do these visual–flavour representations manage to
382 modulate motor output? Comparative literature may provide
383 some evidence for neural networks which connect the OFC with
384 motor regions (Cavada, 2000). Of particular interest for our study is
385 the presence of direct connections between OFC and motor areas
386 involved in arm–hand movement control such as the motor
387 cingulate area 24c/M3, the supplementary motor area F3/M2, the
388 pre-supplementary motor area F6 and the ventral pre-motor area
389 F5. Furthermore, also the primary motor cortex (M1) receives
390 inputs from frontal granular area 12 (Morecraft & van Hoesen,
391 1993). On the basis of the well-known homology between cerebral
392 regions underlying reach-to-grasp movement in monkeys and
393 humans (Begliomini, Caria, Grodd, & Castiello, 2007; Castiello,
394 2005), we suggest that the cortico-cortical connections between
395 OFC and motor areas influencing motor output in non human
396 primates (Bates & Goldman-Rakic, 1993) may also exist in humans
397 and account for the influence of multisensory information on
398 motor behaviour and more specifically on prehensile actions.

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

421

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