

1 Top-down and Bottom-up processes during Observation: Implications for Motor Learning

2

3

4

5

6 James W. Roberts,^{1*} Simon J. Bennett,¹ Digby Elliott,^{1,2} Spencer J. Hayes¹

7

8

9 ¹Brain and Behaviour Laboratory,

10 Liverpool John Moores University, Liverpool, UK

11

12 ²Department of Kinesiology,

13 McMaster University, Ontario, Canada

14

15

16

17

18

19 *Corresponding author

20 Brain and Behaviour Laboratory, Faculty of Science, Liverpool John Moores University,

21 Byrom Street, Liverpool, L3 3AF, UK

22 Tel: +44 (0) 151 904 6237, Fax: +44 (0) 151 904 6284

23 J.W.Roberts@2006.ljmu.ac.uk

24

1 **Abstract**

2 Neurophysiological and behavioural research has linked observational practice to a
3 mirroring mechanism encompassing the action-observation network (AON). Although the
4 original findings indicate that biological stimuli alone activate the AON, recent evidence
5 has shown sensitivity to non-biological stimuli. Thus, the AON is suggested to be
6 influenced by interacting bottom-up and top-down processes. In this review, we describe
7 the multi-functional properties of the AON, and discuss the implications for observational
8 practice and subsequent motor learning.

9

10 **Keywords:** *Observational practice, motor learning, action-observation network*

11

1 **Introduction**

2 Observational practice (OP) is a process by which humans learn motor skills by
3 observing a model, and has been examined using behavioural and neurophysiological
4 paradigms. The former typically requires an observer to watch a [yoked] model physically
5 performing a novel movement task, after which the learner attempts to imitate the action
6 they have just observed. Despite the absence of explicit involvement of the motor system
7 in trial and error learning during OP, data indicate similar motor learning to those who
8 engage in physical practice. This OP effect is not merely limited to the acquisition of
9 behaviours associated with automatic imitation (see Heyes, 2011), but novel motor skills
10 not already represented in an individual's motor repertoire. Indeed, measures of learning
11 following OP include: absolute and relative (Blandin, Lhuisset, & Proteau, 1999) time;
12 inter-and intra-limb transfer of timing information (Hayes, Andrew, Elliott, Roberts, &
13 Bennett, 2012); spatio-temporal properties of cyclical upper-limb tasks (Vogt, 1995);
14 complex sequence knowledge (Bird & Heyes, 2005); force dynamics (Mattar & Gribble,
15 2005; Ong & Hodges, 2010); movement kinematics (Hayes, Timmis, & Bennett, 2009).

16 The majority of the aforementioned behavioural effects have been linked to the
17 general assumption that action-observation and motor-execution are underpinned by a
18 common representational system (e.g., Prinz, 1997). Importantly, however, there is still no
19 widely accepted theory that explains how novel motor skills are acquired during
20 observation. For instance, it was originally thought that higher-level intermediary
21 processes were involved in translating the observed visual stimulus into a motor
22 representation/command (e.g., symbolic coding - Bandura, 1986; amodal processing -
23 Meltzoff & Moore, 1997). More recently, it has been suggested that novel representations
24 developed through imitation learning are associated with sensorimotor transformations

1 that directly recruit the motor system (e.g., mirror-neuron system – Buccino et al., 2004;
2 action-observation network – Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009;
3 associative sequence learning - Heyes & Ray, 2000). Furthermore, the goal-directed
4 theory of imitation (GOADI) suggests that imitation is controlled through cognitive
5 processes (Wohlschläger, Gattis, & Bekkering, 2003) which decompose the observed
6 movement into a hierarchy of goals, with the primary goal driving subsequent action
7 reproduction (Bekkering, Wohlschläger, & Gattis, 2000). The following review does not
8 intend to debate these theories (see Heyes, 2011; Heyes & Bird, 2007), or discuss the
9 evidence supporting OP. Thus, we will add to the current understanding of OP by
10 reviewing the neural processes which underpin motor learning within the
11 action-observation network. Following this, we review the contribution of bottom-up
12 (stimulus-driven) and top-down (goal-directed) processes during OP. Finally, we suggest
13 some implications for use in sport and motor learning settings, whilst providing possible
14 research directions.

15

16 **Motor learning within the action-observation network**

17 Since the discovery of F5 mirror neurons in monkey (e.g., di Pellegrino, Fadiga,
18 Fogassi, Gallese, & Rizzolatti, 1992) there have been over 100 studies examining the
19 suggestion that a mirror mechanism is present in the human brain (see Caspers, Zilles,
20 Laird, & Eickhoff, 2010). The first direct evidence was reported by Fadiga, Fogassi, Pavesi
21 and Rizzolatti (1995), who measured motor-evoked potentials (MEPs) induced by
22 transcranial magnetic stimulation (TMS) during the observation of upper-limb movements.
23 The data indicated motor system excitation when an observer viewed another person
24 making a movement, but more importantly that the MEPs were similar to those recorded

1 during the execution of the same movement. Subsequently, it was shown that motor
2 excitability was scaled and temporally linked to the observed kinematic events, such that a
3 motor plan was constructed whilst the movement unfolded (Gangitano, Mottaghy, &
4 Pascual-Leone, 2001). More recently, data from functional magnetic resonance imaging
5 (fMRI) experiments have mapped the rostral part of the inferior parietal lobule (aIPL), pars
6 opercularis of the inferior frontal gyrus (IFG), and adjacent ventral premotor cortex (vPM),
7 as being the core mirror regions (MNS) during imitation (Iacoboni et al., 1999). In addition,
8 it has been reported that the posterior part of the superior temporal sulcus (pSTS) is
9 activated during action-observation (Iacoboni et al., 2001), although this region does not
10 feature mirror properties. Together, these regions form the mirror-neuron circuit, or the
11 action-observation network (AON) (Cross et al., 2009). The precise function of these
12 regions has received much debate with suggestions that the pSTS supplies a visual
13 description to the fronto-parietal mirror circuit, where IFG/vPM codes the goal-directed
14 information (higher-level) and aIPL codes the motoric aspects of the movement
15 (lower-level) (Iacoboni, 2005). However, there are data that indicate the frontal mirror
16 regions code the kinematics, and the parietal mirror regions code the goal (see Hamilton,
17 2008).

18 Recent investigations have examined the role of this network during imitation
19 learning (i.e., continuous process of observation followed by execution – also referred to
20 as observational learning) and OP (i.e., observation across a series of trials featuring no
21 motor execution). For example, Buccino et al. (2004) had participants observe (event 1),
22 prepare (event 2) and execute (event 3) novel guitar chords during an fMRI experiment.
23 They reported an increase in neural activity within the AON during observation (event 1)
24 compared to rest (event 4). Subsequent imitation revealed activation in corresponding

1 regions. Importantly, they also recorded activity in the dorsolateral prefrontal cortex
2 (DLPFC) during preparation, which was interpreted as being the region that controlled the
3 selection and re-configuration of pre-existing motor primitives into a novel representation
4 of the observed act. Thus, these data presented a neural substrate linking sensorimotor
5 processes associated with activating previously acquired motor representations (i.e.,
6 action recognition) and the acquisition of novel motor skills. Vogt et al. (2007) tested this
7 hypothesis by manipulating the presence of learned or unlearned guitar chords after OP
8 and showed that DLPFC activity was greater when observers viewed the unlearned guitar
9 chords. In a follow up study (Higuchi, Holle, Roberts, Eickhoff, & Vogt, 2012), the activity
10 recorded in DLPFC during OP positively correlated with the changes in motor
11 performance (i.e., chord response times). Importantly, the authors reported functional
12 connectivity between the DLPFC and AON, with the associated neural activity
13 progressively decreasing as learners became more skilled at the task. Thus, at the skilled
14 level, it would seem that more direct mirroring processes govern the relationship between
15 action-observation and motor-execution (Calvo-Merino, Glaser, Grezes, Passingham, &
16 Haggard, 2005). These data extend suggestions of sensorimotor transformations
17 enabling motor learning through observation (e.g., Bird & Heyes, 2005; Mattar & Gribble,
18 2005), by incorporating higher-level supervisory control mechanisms.

19 Whilst the AON undoubtedly contributes to OP there are data that indicate the
20 processes that operate during OP are not precisely the same as those involved during
21 physical practice (Hayes et al., 2012; Higuchi et al., 2012; Ong & Hodges, 2010). For
22 example, Ong and Hodges (2010) reported increased 'after-effects' (i.e., incompatible
23 non-intended remnants of movement developed in a perturbed visuo-motor environment)
24 for physical practice groups compared to a standard OP group. Furthermore, having first

1 confirmed learning of a motor sequence timing task through OP or physical practice
2 (Hayes et al., 2012), we found that only the physical practice group were able to
3 successfully transfer to an intermanual *mirror* sequence condition (i.e., homologous motor
4 commands - opposing visuo-spatial coordinates and effector). These differences can be
5 explained by the addition of sensorimotor refference from an operating effector(s) during
6 physical practice. This refference is compared to the predicted sensory consequences
7 (forward model) in order to update and refine the sensorimotor representation (inverse
8 model) developed during motor learning (see Elliott et al., 2010). Without sensorimotor
9 refference, the predominant source of information represented during observation is
10 visual, which alters the comparison process. We do not suggest that this implies motor
11 regions (e.g., primary motor cortex; premotor cortices; supplementary motor area) are not
12 recruited during OP, but rather that a representation(s) developed through OP is primarily
13 based on visuo-spatial codes as opposed to motor codes (e.g., Mattar & Gribble, 2005).

14

15 **Bottom-up processes**

16 A common indicator of bottom-up processing of the AON during observation is the
17 implicit sensitivity to specialised visual information. Indeed, the AON preferentially
18 responds to the observation of human stimuli, rather than non-human stimuli (see a
19 review by Press, 2011 on the AON and biological tuning). Hence, the AON is thought to be
20 biologically tuned, which makes sense given it develops through sensorimotor experience
21 (Heyes, 2005) and underpins many socio-cognitive functions (Gallese & Goldman, 1998).
22 From a motor learning perspective, the biological tuning of the AON may originate from
23 connections to pSTS (Iacoboni, 2005), which is a region activated during the perception of
24 biological motion (Bonda, Petrides, Ostry, & Evans, 1996). Thus, Iacoboni suggested that

1 during OP, visual information projected from pSTS provides a visual description of the
2 observed action to the frontoparietal mirror regions for subsequent action coding. Based
3 on this suggestion, it is reasonable to predict that observing biological motion may
4 facilitate the learning of novel motor skills.

5 Data from neurophysiological experiments confirm preferential coding of biological
6 stimuli in the AON. For example, EEG data revealed increased interregional coherence of
7 alpha-band activity in the frontoparietal central regions during the observation of finger
8 movements (Holz, Doppelmayr, Klimesch, & Sauseng, 2008). Indeed, corresponding
9 interregional coherence during observational learning correlated with performance
10 accuracy scores of a novel finger sequence task (van der Helden, van Schie, &
11 Rombouts, 2010). Moreover, it is not just the global properties of biological stimuli (e.g.,
12 human form) that tune the AON. For instance, the AON responds specifically to biological
13 motion that adheres to normal kinematic laws such as the two-thirds power law of motion
14 (Dayan et al., 2007; Casile et al., 2010). This latter finding is important as it indicates the
15 AON encodes [ecologically valid] aspects of biological movements, which in the case of
16 OP, may be the speed and temporal characteristics of complex motor skills.

17 Initial behavioural evidence to indicate biological tuning came from automatic
18 imitation paradigms (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Stürmer,
19 Aschersleben, & Prinz, 2000), which examined stimulus-response compatibility in the
20 presence of biological (finger movements) or non-biological stimuli (symbolic cues). Brass
21 et al. (2000) reported finger lifting movements were initiated faster when the imperative
22 stimulus cue was compatible with the model compared to viewing an incompatible model
23 (e.g., finger tapping movement). This facilitation is thought to reflect automatic activation
24 of motor codes that correspond to the observed action. Supporting this postulation is

1 evidence of unintended movement deviation of arm movements when concurrently
2 observing orthogonal human arm movements compared to robot arm movements (Kilner,
3 Paulignan, & Blakemore, 2003). This effect was termed ‘motor contagion’ (Blakemore &
4 Frith, 2005) based on the suggestion that the biological properties of the observed human
5 movement directly activated a corresponding action representation within the observer’s
6 motor repertoire.

7 In addition to stimulus-response and motor interference paradigms, the data from
8 voluntary imitation experiments indicate that observers copy the movement kinematics
9 (speed) displayed by a human model (Wild, Poliakoff, Jerrison, & Gowen, 2010) and
10 biological-dot motion stimulus (Bisio, Stucchi, Jacono, Fadiga, & Pozzo, 2010). The latter
11 effect shows that coding of biological motion is not limited to, or reliant upon, the presence
12 of human form (Press, 2011). Thus, and irrespective of the stimulus type, it was
13 suggested that movement kinematics are coded through lower-level mechanisms (e.g.,
14 direct-matching hypothesis; Rizzolatti, Fogassi & Gallese, 2001). We have found similar
15 effects in our OP experiments involving motor timing tasks (e.g., Hayes et al., 2009).
16 Specifically, movements initiated by observers produced similar kinematics (i.e.,
17 proportion of time to peak velocity and peak velocity) as those executed by the learning
18 models (i.e., those that physically practised the motor timing task). In line with a
19 direct-matching prediction, we suggested that motor timing could have been learned by
20 coding biological motion through lower-level regions of the AON (i.e., bottom-up
21 propagation based on motor resonance). However, because our task required learners to
22 execute prototypical aiming actions (i.e., a simple upper limb movement directed to a
23 target) the motor timing may have been influenced by higher-level goal-related processes
24 (action-reconstruction hypothesis; Csibra, 2007). That is, both the model and observer

1 may have coincidentally initiated the most efficient means to achieve a common goal (i.e.,
2 timing). It is noteworthy that the aforementioned voluntary imitation and OP studies differ
3 to automatic imitation due to the additional processes influencing motor output (e.g.,
4 cognitive mediation). This has recently been recognised in the ideomotor model of
5 imitation (Spengler, Brass, Kühn, & Schütz-Bosbach, 2010), where factors influencing
6 perception (e.g., attention) and movement (e.g., inhibitory control) are suggested to
7 mediate the automatic activation of sensorimotor representations (see Figure 5 published
8 in Spengler et al. 2010).

9 Using a novel movement sequence timing paradigm, we have examined the
10 potential confluence between the higher-level demands and motor constraints of the task
11 by dissociating the timing goal (relative time) from the means of achieving the timing goal
12 (Roberts et al., in prep). In a *natural* condition, participants observed a model displaying a
13 prototypical aiming movement involving a relatively bell-shaped velocity profile (peak
14 velocity occurred at ~50% of the movement). Meanwhile, the *unnatural* condition involved
15 the observation of an atypical (but achievable) velocity profile (e.g., peak velocity occurred
16 at ~95% of the movement). It is important to note that we kept the timing goal consistent
17 across the two model conditions to examine whether observers learned the lower-level
18 kinematics to subsequently obtain the timing goal, or emulated the timing goal by
19 executing the most efficient means (i.e., not learning the *unnatural* kinematics). The data
20 from a series of five experiments indicated that lower-level, *unnatural* biological motion
21 was indeed learned. However, this process was not solely based on lower-level
22 mechanisms in the motor system, but was also influenced by top-down processes
23 associated with attention and hierarchical action coding. Thus, these data indicated that
24 OP involves the contribution of both bottom-up and top-down processes, as opposed to a

1 sole operating sensorimotor, or cognitive, mechanism.

2 The fact that coding of biological motion is subject to top-down, interpretative
3 (human and point-light models) and higher-level processes supports the
4 neurophysiological findings of similar levels of activity in the AON following observation of
5 human and robotic reaching and grasping actions (Gazzola, Rizzolatti, Wicker, & Keysers,
6 2007). In addition, data recorded from aplasic participants, who born without hands, show
7 increased activity in the AON during the observation of hand actions (Gazzola, van der
8 Worp, et al., 2007). Interestingly, though, the region[s] activated was not an anatomical
9 hand representation but rather an area responsible for executing either a foot and mouth
10 action. It was therefore concluded the primary function of the AON was to code the goal of
11 the action rather than the means in which the goal was achieved.

12 Consistent with the goal-matching properties of the AON is data collected from
13 goal-directed imitation tasks where infants predominantly grasp the correct ear, but do so
14 using an incorrect ipsilateral arm movement (Bekkering et al., 2000). However, when
15 instructed to copy a similar contralateral arm movement with the goal to grasp an ear
16 removed, participants successfully reproduced this arm movement (Gleissner, Meltzoff,
17 Bekkering, 2000). These data underpin the GOADI theory, which states an observed
18 action is decomposed into a hierarchy of task goals, with the primary goal being imitated
19 at the expense of the means (Wohlschläger et al., 2003). Moreover, when end-state
20 information is removed, the 'means' subsequently become the primary goal. Support for
21 this model of OP was reported in a study by Hayes, Ashford and Bennett (2008) where
22 school-aged children (10-11 years) successfully learned the means of an observed action
23 in order to attain the outcome goal of a novel juggling cascade. That is, the necessity of
24 the means can propagate certain action features up the action hierarchy and thereby

1 facilitate motor learning.

2 Together, these data indicate the AON is not solely biased to automatically map
3 biological motion onto the motor system during OP. Instead, it would seem to suggest that
4 the AON responds to an observed action at multiple levels by engaging bottom-up
5 (stimulus-driven, motor resonance) and top-down (goal-directed, inferential, attention)
6 processes.

7

8 **Top-down modulation**

9 The confirmation that top-down factors influence action-observation has been
10 reported in tasks that have manipulated attention (Bach, Peatfield, & Tipper, 2007),
11 context (Liepelt, von Cramon, & Brass, 2008) and belief (Liepelt & Brass, 2010; Stanley,
12 Gowen, & Maill, 2007). For example, the unintended movement deviation (i.e., motor
13 contagion) reported during concurrent observation of orthogonal dot-motion displays was
14 enhanced when participants were informed the stimuli were human-generated compared
15 to computer-generated (Stanley et al., 2007). These effects were independent of the
16 velocity characteristics (i.e., two-thirds power law or constant velocity) of the dot motion
17 and indicate that the system responsible for processing biological motion can also be
18 engaged through the human interpretation (i.e., belief) of an inanimate point-light dot.
19 Moreover, even when controlling the perceptual similarity between the stimulus and the
20 effector operated by the observer, the attribution of human movement via belief continues
21 to prime the motor system during automatic imitation (Liepelt & Brass, 2010). This led to
22 the 'gating hypothesis', which predicts observed stimuli believed to be biological gains
23 privileged access to the AON. The aforementioned effects indicate that motor contagion
24 and/or automatic imitation are not default behaviours independent of higher-level

1 cognitive processes.

2 A neural substrate for these top-down processes has been proposed based on the
3 inhibition of automatic imitation in frontal lesion patients (Brass, Derrfuss, Mathes-von
4 Cramon, & von Cramon, 2003). Neuro-imaging data indicate the anterior frontomedian
5 cortex (aFMC) and temporo-parietal junction (TPJ) provide top-down control (Brass,
6 Derrfuss, & von Cramon, 2005). Moreover, these top-down processes have been shown
7 to mediate bottom-up processes during action-observation (Spengler, von Cramon, &
8 Brass, 2010). Therefore, given the similarity in the mechanisms forwarded in sensorimotor
9 models of imitation learning (Buccino et al., 2004), OP (Higuchi et al., 2012) and automatic
10 imitation, it is reasonable to predict top-down processes may impact motor learning by
11 observing. Therefore, future research on OP should examine whether top-down
12 processes modulate bottom-up processes in a motor learning context.

13 In addition to top-down control, the aforementioned neural regions may also
14 support mentalizing functions (Frith & Frith, 2003). This was demonstrated in recent
15 behavioural (Leighton, Bird, Orsini, & Heyes, 2010; Wang, Newport, & Hamilton, 2011)
16 and neurophysiological (Wang, Ramsey, & Hamilton, 2011) experiments, which
17 manipulated social cues/primes. For example, Leighton et al. (2010) conducted a two-part
18 experiment where participants first completed a social priming task followed by an
19 automatic imitation task. The priming task involved reading and constructing sentences
20 from words that encouraged a pro-social attitude (e.g., *cooperate or team*) or an
21 anti-social attitude (e.g., *alone or enemy*). The data showed a robust motor priming effect
22 featuring faster response times following a pro-social prime compared to an anti-social
23 prime. A similar manipulation revealed enhanced motor priming following a direct gaze
24 condition (eye gaze of model directed towards observer), compared to an averted gaze

1 condition (eye gaze of model directed away from observer) (Wang, Newport, & Hamilton,
2 2011). These effects were related to activity of medial prefrontal cortex (mPFC), STS and
3 IFG, including a functional connectivity between mPFC and STS (Wang, Ramsey, &
4 Hamilton, 2011). Although there is no evidence to indicate social cues/primes regulate
5 OP, these data indicate that the top-down processes mediating bottom-up mechanisms
6 are closely linked to social functions. Thus, we are currently exploring this issue using a
7 social priming paradigm (e.g., direct or averted gaze) in which participants are required to
8 learn a novel aiming movement that contains *unnatural* (experimental condition) or *natural*
9 (control condition) movement kinematics. We predict that participants will learn the
10 *unnatural* kinematics more accurately in the *direct* condition because eye gaze will impact
11 the top-down processes (mPFC) and subsequently mediate the bottom-up mechanisms
12 required for coding the *unnatural* biological motion.

13

14 **Conclusion**

15 A review of neurophysiological and behavioural literature related to OP, indicates
16 that this process is mediated by a mirror mechanism located in aIPL and IFG/vPM.
17 Together, these neural regions make up part of the AON, which in combination with
18 working memory processes located in DLPFC, can develop novel motor representations.
19 Rather than simply being sensitive to biological stimuli (bottom-up processes), it is now
20 recognised that the AON also responds to non-biological stimuli if preceded by primes that
21 influence belief or social belonging (top-down processes). In this way, the bottom-up
22 processes operating during OP can be modulated by top-down processes. Hence, sport
23 scientists, coaches and educators should consider the interaction of bottom-up and
24 top-down processes during the design and implementation of OP. Specifically, the

1 emergence of an overlap between mentalizing and top-down functions means the
2 manipulation of social (social cues; instructions) or contextual information may influence
3 bottom-up processing of biological motion in order to facilitate the acquisition of motor
4 skills.
5

1 **References**

2 Bach, P., Peatfield, N. A., & Tipper, S. P. (2007). Focusing on body sites: the role of
3 spatial attention in action perception. *Experimental Brain Research*, 178, 509-517.

4
5 Bandura, A. (1986). *Social foundations of thought and action: A social cognitive theory*.
6 Englewood Cliffs, NJ: Prentice-Hall.

7
8 Bekkering, H., Wohlschläger, A., & Gattis, M. (2000). Imitation of gestures in children is
9 goal-directed. *The Quarterly Journal of Experimental Psychology. A, Human*
10 *Experimental Psychology*, 53, 153-164.

11
12 Bird, G., & Heyes, C. (2005). Effector-dependent learning by observation of a finger
13 movement sequence. *Journal of Experimental Psychology. Human Perception and*
14 *Performance*, 31, 262-275.

15
16 Bisio, A., Stucchi, N., Jacono, M., Fadiga, L., & Pozzo, T. (2010). Automatic versus
17 voluntary motor imitation: effect of visual context and stimulus velocity. *PloS One*, 5,
18 e13506.

19
20 Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action.
21 *Neuropsychologia*, 43, 260-267.

22

- 1 Blandin, Y., Lhuisset, L., & Proteau, L. (1999). Cognitive processes underlying
2 observational learning of motor skills. *The Quarterly Journal of Experimental*
3 *Psychology, 52*, 957-979.
- 4
- 5 Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human
6 parietal systems and the amygdala in the perception of biological motion. *The*
7 *Journal of Neuroscience, 16*, 3737-3744.
- 8
- 9 Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between
10 observed and executed finger movements: comparing symbolic, spatial, and
11 imitative cues. *Brain and Cognition, 44*, 124-143.
- 12
- 13 Brass, M., Derrfuss, J., Matthes-von Cramon, G., & von Cramon, D. Y. (2003). Imitative
14 response tendencies in patients with frontal brain lesions. *Neuropsychology, 17*,
15 265-271.
- 16
- 17 Brass, M., Derrfuss, J., & von Cramon, D. Y. (2005). The inhibition of imitative and
18 overlearned responses: a functional double dissociation. *Neuropsychologia, 43*,
19 89-98.
- 20
- 21 Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., et al. (2004). Neural
22 circuits underlying imitation learning of hand actions: an event-related fMRI study.
23 *Neuron, 42*, 323-334.
- 24

- 1 Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2005).
2 Action observation and acquired motor skills: an fMRI study with expert dancers.
3 *Cerebral Cortex*, *15*, 1243-1249.
4
- 5 Casile, A., Dayan, E., Caggiano, V., Hendler, T., Flash, T., & Giese, M., A. (2009).
6 Neuronal encoding of human kinematic invariants during action-observation. *Cerebral*
7 *Cortex*, *20*, 1647-1655.
8
- 9 Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of
10 action-observation and imitation in the human brain. *Neuroimage*, *50*, 1148-1167.
11
- 12 Cross, E. S., Kraemer, D. J., Hamilton, A. F., Kelley, W. M., & Grafton, S. T. (2009).
13 Sensitivity of the action observation network to physical and observational learning.
14 *Cerebral Cortex*, *19*, 315-326.
15
- 16 Csibra, G. (2007). Action mirroring and action understanding: an alternative account. In.
17 P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Sensorimotor foundations of Higher*
18 *Cognition, Attention and Performance XXII* (pp. 435-459). Oxford: University Press.
19
- 20 Dayan, E., Casile, A., Levitt-Binnun, N., Giese, M. A., Hendler, T., Flash, T. (2007). Neural
21 representations of kinematics laws of motion: evidence for action-perception
22 coupling. *Proceedings of the National Academy of Science*, *104*, 20582-20587.
23

- 1 di Pelligrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992).
2 Understanding motor events: a neurophysiological study. *Experimental Brain*
3 *Research, 91*, 176-180.
4
- 5 Elliott, D., Hansen, S., Grierson, L. E. M., Lyons, J., Bennett, S. J., & Hayes, S. J. (2010).
6 Goal-directed aiming: two components but multiple processes. *Psychological*
7 *Bulletin, 136*, 1023-1044.
8
- 9 Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action
10 observation: a magnetic stimulation study. *Journal of Neurophysiology, 73*,
11 2608-2611.
12
- 13 Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing.
14 *Philosophical Transactions of the Royal Society of London. Series B, Biological*
15 *Sciences, 358*, 459-473.
16
- 17 Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of
18 mind-reading. *Trends in Cognitive Sciences, 2*, 493-501.
19
- 20 Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2001). Phase-specific modulation
21 of cortical motor output during movement observation. *NeuroReport, 12*, 1489-1492.
22

- 1 Gazzola, V., Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: the
2 mirror neuron system responds to human and robotic actions. *Neuroimage*, *35*,
3 1674-1684.
4
- 5 Gazzola, V., van der Worp, H., Mulder, T., Wicker, B., Rizzolatti, G., & Keysers, C. (2007).
6 Aphasics born without hands mirror the goal of hand actions with their feet. *Current*
7 *Biology*, *17*, 1235-1240.
8
- 9 Gleissner, B., Meltzoff, A. N., & Bekkering, H. (2000). Children's coding of human action:
10 cognitive factors influencing imitation in 3-year olds. *Developmental Science*, *3*,
11 405-414.
12
- 13 Hamilton, A. F. (2008). Emulation and mimicry for social interaction: a theoretical
14 approach to imitation in autism. *The Quarterly Journal of Experimental Psychology*,
15 *61*, 101-115.
16
- 17 Hayes, S. J., Andrew, M., Elliott, D., Roberts, J. W., & Bennett, S. J. (2012). Dissociable
18 contributions of motor-execution and action-observation to intermanual transfer.
19 *Neuroscience Letters*, *506*, 346-350.
20
- 21 Hayes, S., J., Ashford, D., & Bennett, S. J. (2008). Goal-directed imitation: The means to
22 an end. *Acta Psychologica*, *127*, 407-415.
23

- 1 Hayes, S. J., Timmis, M. A., & Bennett, S. J. (2009). Eye movements are not a
2 prerequisite for learning movement sequence timing through observation. *Acta*
3 *Psychologica*, 131, 202-208.
- 4
- 5 Heyes, C. (2005). Imitation by association. In. S. Hurley & N. Chater (Eds.), *Perspective*
6 *on imitation: from neuroscience to social science* (pp. 157-176). Cambridge, MA:
7 MIT Press.
- 8
- 9 Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, 137, 463-483.
- 10
- 11 Heyes, C., & Bird, G. (2007). Mirroring, association, and the correspondence problem. In.
12 P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Sensorimotor foundations of Higher*
13 *Cognition, Attention and Performance XXII* (pp. 461-479). Oxford: University Press.
- 14
- 15 Heyes, C. M., & Ray, E. D. (2000). What is the significance of imitation in animals?
16 *Advances in the Study of Behaviour*, 29, 215-245.
- 17
- 18 Higuchi, S., Holle, H., Roberts, N., Eickhoff, S. B., & Vogt, S. (2012). Imitation and
19 observational learning of hand actions: prefrontal involvement and connectivity.
20 *NeuroImage*, 59, 1668-1683.
- 21
- 22 Holz, E. M., Doppelmayr, M., Klimesch, W., & Sauseng, P. (2008). EEG correlates of
23 action observation in humans. *Brain Topography*, 21, 93-99.
- 24

1 Iacoboni, M. (2005). Neural mechanisms of imitation. *Current Opinion in Neurobiology*,
2 15, 632-637.

3

4 Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., et al.
5 (2001). Reafferent copies of imitated actions in the right superior temporal cortex.
6 *Proceedings of the National Academy of Sciences of the United States of America*,
7 98, 13995-13999.

8

9 Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G.
10 (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526-2528.

11

12 Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed
13 biological movement on action. *Current Biology*, 13, 522-525.

14

15 Leighton, J., Bird, G., Orsini, C., & Heyes, C. (2010). Social attitudes modulate automatic
16 imitation. *Journal of Experimental Social Psychology*, 46, 905-910.

17

18 Liepelt, R., & Brass, M. (2010). Top-down modulation of motor priming by belief about
19 animacy. *Experimental Psychology*, 57, 221-227.

20

21 Liepelt, R., Cramon, D. Y., & Brass, M. (2008). What is matched in direct matching?
22 Intention attribution modulates motor priming. *Journal of Experimental Psychology*.
23 *Human Perception and Performance*, 34, 578-591.

24

- 1 Mattar, A. A., & Gribble, P. L. (2005). Motor learning by observing. *Neuron*, *46*, 153-160.
- 2
- 3 Meltzoff, A. N., & Moore, M. K. (1997). Explaining facial imitation: a theoretical model.
- 4 *Early Development and Parenting*, *6*, 179-192.
- 5
- 6 Ong, N. T., & Hodges, N. J. (2010). Absence of after-effects for observers after watching a
- 7 visuomotor adaptation. *Experimental Brain Research*, *205*, 325-334.
- 8
- 9 Press, C. (2011). Action observation and robotic agents: learning and anthropomorphism.
- 10 *Neuroscience and Biobehavioral Reviews*, *35*, 1410-1418.
- 11
- 12 Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive*
- 13 *Psychology*, *9*, 129-154.
- 14
- 15 Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neuropsychological mechanisms
- 16 underlying the understanding and imitation of action. *Nature Reviews Neuroscience*,
- 17 *2*, 661-670.
- 18
- 19 Spengler, S., Brass, M., Kühn, S., & Schütz-Bosbach, S. (2010). Minimizing motor mimicry
- 20 by myself: Self-focus enhances online action-control mechanisms during motor
- 21 contagion. *Consciousness and Cognition*, *19*, 98-106.
- 22

- 1 Spengler, S., von Cramon, D. Y., & Brass, M. (2010). Resisting motor mimicry: control of
2 imitation involves processes central to social cognition in patients with frontal and
3 temporo-parietal lesions. *Social Neuroscience*, 5, 401-416.
- 4
- 5 Stanley, J., Gowen, E., & Miall, R. C. (2007). Effects of agency on movement interference
6 during observation of a moving dot stimulus. *Journal of Experimental Psychology*.
7 *Human Perception and Performance*, 33, 915-926.
- 8
- 9 Stürmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence effects with manual
10 gestures and postures: a study of imitation. *Journal of Experimental Psychology*, 26,
11 1746-1759.
- 12
- 13 van der Helden, J., van Schie, H. T., & Rombouts, C. (2010). Observational learning of
14 new movement sequences is reflected in fronto-parietal coherence. *PloS One*, 5,
15 e14482.
- 16
- 17 Vogt, S. (1995). On relations between perceiving, imagining and performing in the
18 learning of cyclical movement sequences. *British Journal of Psychology*, 86,
19 191-216.
- 20
- 21 Vogt, S., Buccino, G., Wohlschläger, A., Canessa, N., Shah, N. J., Zilles, K. et al. (2007).
22 Prefrontal involvement in imitation learning of hand actions: effects of practice and
23 expertise. *NeuroImage*, 37, 1371-1383.
- 24

- 1 Wang, Y., Newport, R., Hamilton, A. F. (2011). Eye contact enhances mimicry of
2 intransitive hand movements. *Biology Letters*, 7, 7-10.
3
- 4 Wang, Y., Ramsey, R., & Hamilton, A. F. (2011). The control of mimicry by eye contact is
5 mediated by medial prefrontal cortex. *The Journal of Neuroscience*, 31,
6 12001-12010.
7
- 8 Wild, K. S., Poliakoff, E., Jerrison, A., & Gowen, E. (2010). The influence of goals on
9 movement kinematics during imitation. *Experimental Brain Research*, 204, 353-360.
10
- 11 Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action
12 perception in imitation: an instance of the ideomotor principle. *Philosophical
13 Transactions of the Royal Society of London. Series B, Biological Sciences*, 358,
14 501-515.